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NAME OF AUTHOR/*NOM DE L'AUTEUR* RAFFAELLA MORGANTIN.

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NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* A. L. STEINER

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DIFFERENTIAL SEED-PECKING RESPONSES BY JAPANESE QUAIL: AN EXPERIMENTAL APPROACH TO BATESIAN COLOR MIMICRY

by

© RAFFAELLA MORGANTINI

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Differential seed-pecking responses by Japanese quail: An experimental approach to Batesian color mimicry" submitted by Raffaella Morgantini in partial fulfilment of the requirements for the degree of Master of Science

.....A. Stewart.....
Supervisor
...Richard C. Fox.....
.....
.....W. G. Evans.....
.....

Date. Feb. 24. 1978

ABSTRACT

In the present study a series of artificial pairs of mimics and models were tested in order of increasingly closer similarity. In the two main experiments run (A and B) caged Japanese quail (Coturnix coturnix japonica) were the predators, wheat seeds upon colored substrates were the prey, seed-pecking rates were used as an index of predatory attacks, and the "model" seeds were treated with quinine. The successive presentation of prey generally involved two different colors. The same ten birds were tested throughout each experiment.

Each experiment included, in succession, two phases; during the final phase (2) the edible ("mimic") and the unpalatable ("model") seeds were tested together. In the initial phase (1) only edible seeds were used, variously associated with the same pairs of color substrates of Phase 2.

Coloration of the substrates per se did not generally appear to affect rates of pecking; it is suggested that the one possible instance of such an effect could be better explained by other factors. The substrates' coloration appeared however to significantly affect pecking rates, by depressing it during the first day of presentation of a novel color pair. Novelty effects are suggested as the possible explanation for such a pattern; their wearing off with time is considered for Experiment A, and their

interactions with other effects is discussed for Experiment B.

With first introduction of the unpalatable seeds, initially effects were noted that could not be attributed to mimetic similarity of the pairs of color substrates. The unpalatable seeds were attacked more often, and the edible seeds less often, than during the successive sessions of the same color pair. The introduction of punishment is here suggested as the most important contributing factor.

With increases in similarity in Experiment A an apparently converging pattern between frequencies of attack for the mimics and for their corresponding models was recorded; such findings are discussed in terms of theoretical expectations. The failure to observe the above pattern replicated in Experiment B for the mimics is examined in function of novelty effects possibly retained from the preceding Phase 1.

Direct discrimination between the quinine treated ("model") and the untreated ("mimic") seeds was indicated in absence of differential color cues from the substrates. The effects are discussed for such very fine discrimination abilities, that had previously been unsuspected in other experimental mimicry studies. In an attempt to eliminate the latter effects, the seeds were rendered available, in a different design, only upon completition of a seed-pecking routine. The seeds obtained thereafter were edible or unpalatable, depending on the color of the keys. Even this

technique appeared, however, not to satisfactorily eliminate the effects of direct discrimination, the latter being often merely postponed until the seeds became visible.

It is concluded that, in experimental mimicry studies, a greater attention should be paid to the behavioral characteristics of the predators, in function of all the other fear-evoking stimuli simultaneously present. The definitions and extents of the concept of mimicry are synthetically discussed in this light.

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1. INTRODUCTION AND BACKGROUND INFORMATION

Rettenmeyer (1970, pp 43-44) lists as follows the major characteristics of Batesian mimicry: "(a) a species, the model, is unpalatable to predators; (b) a second species, the mimic, is palatable to predators but...it resembles the model so closely that potential predators are deceived and leave it alone; (c) the mimics are less abundant than the models; (d) the mimics must be found at the same place and time as the models; (e) the model and the mimic are conspicuous or readily seen by potential predators; and (f) the predators learn or associate unpalatability with color-pattern of the model" The author indicates (a), (b) and (f) as being essential.

Almost any characteristics of the model can be copied by the mimic - e.g., scent, behavior, sound, color, pattern, etc., alone or in combinations (Wickler, 1968). In the present work I have focused my attention on increasingly efficient color mimicry, such as could be found among diurnal imago Lepidoptera, and on related experimental studies.

The evolutionary impact of predation on mimic-model systems is generally the most stressed parameter in mimicry studies. A predator's abilities and behavior are often only minimally considered, and have been given little attention in many experimental designs. For instance, Coppinger in

1969 pointed out that "novelty" effects might decrease the frequency of attacks on edible prey regardless of the presence of "mimetic" factors. Furthermore, during the present study, I found finer discrimination abilities than previously suspected in predators used in mimicry experiments (confirmed by Terhune, 1976). Failure to recognize and control for these factors in previous studies may have severely reduced the significance of a whole body of collected evidence.

In the present study an effort was made to give a greater emphasis to the predator's direct influence, by considering a number of other factors, potentially interactive with mimicry effects, which may decrease or increase frequency of attacks on prey.

For the sake of clarity in the following paragraphs I will first examine separately the three components of a predator-mimic-model system.

a) Predator

Predation is considered to be the selective agent for the evolution of mimicry and warning colorations. Factors such as: a) built-in preferences; b) learning mechanisms; c) discrimination abilities; d) "emotionality"; e) motivation; f) sensory perception; etc., might all play a great part in determining, both in nature and in the

laboratory, the functioning of mimic-model-predator systems. Each of these factors, with the possible exception of a), constitutes by itself a whole active field of psychological research; some examples of extensive reviews are: Thorpe (1969) for (a); Medin, et al., (1976) for (b); Gilbert and Sutherland (1969) for (c); Brown (1961) for (e); etc.

From a more ethological standpoint, the effects of different factors on predatory strategies with respect to mimic-model systems have been examined by several authors: memory (Rothschild, 1964); responses to prey density (Holling, 1965); search image and attention (e.g., Dawkins, 1971 a,b); fear and emotionality (Hogan, 1965); effects of presence of alternate prey (Schuler, 1974), etc.

It can also be a complex problem to attempt to generalize from laboratory experiments to a natural situation. In the laboratory, the prey is usually static, close and clearly visible. Such a situation could overemphasize the discrimination part of the prey selection process and underestimate the "error" part of it. Furthermore, the prey is often presented in a constant location, thus eliminating the search stage and focusing the attention of the predator. Attempts to overcome such limitations have involved offering of artificial models and mimics to free-living urban birds (e.g., O'Donald and Pilecki, 1970) and releasing/recapturing of butterflies artificially painted to resemble existing wild models

(e.g., Brower, et al., 1967; Cook, et al., 1969). These techniques, however, appear in need of further refinement (Waldbauer and Sternburg, 1975).

b) Model

A broad range of "distasteful" qualities in unpalatable prey has been demonstrated (see Rothschild and Kellett, 1973 for a review), and even individuals of the same species may vary considerably in this respect (Brower and Moffitt, 1974). Duncan and Sheppard (1965) demonstrated an increased protection to the mimics of more distasteful models.

Fisher in 1930 suggested the hypothesis that what "gives rise to warning colours generally.." is to avoid being confused "...with palatable species.." (p. 148). Other authors, however, seem to consider the "conspicuousness" of warning colors as related to the environment, rather than to other species. The term "conspicuous" appears then somewhat ambiguous, and I propose to define the warningly colored prey as "contrasting" with the environment and/or "distinctive" from other species, in cases where ambiguity might arise.

Warning of unpalatability is often associated with the "warm" colors - yellow, orange, red - or with the most intense tones - black and white - (see Cott, 1940, for a

detailed review). Other colors might, however, be present alone or in combination.

Predators' avoidance of warningly colored species has been suggested as due either to built-in mechanisms or to learning, or both. Examples of built-in color preferences have been demonstrated in naive birds with respect to ambient-related choices (e.g., Hess and Gogel, 1954, in chicks and Kovach, 1974, in quail). Pecking preferentially directed toward certain color spots has been demonstrated in gull chicks as an innate releasing mechanism (IRM) (Tinbergen and Perdeck, 1950). It is, however, doubtful to what extent such findings can be generalized. The extent and the importance, if any, of built-in responses to warning colors appears to be still largely unknown.

Associative learning abilities of birds have been, on the other hand, demonstrated again and again and constitute an active field of psychological studies (e.g., Sutherland and Mackintosh, 1971). The mass of experimental evidence accumulated through mimicry studies can leave little doubt as to the extent of the role of learning. Furthermore, a dramatic decrease in the frequency of attacks on "pseudo-warningly" (mimetically) colored insects following exposure to the similarly colored, but unpalatable, model has repeatedly been demonstrated (e.g., Brower, et al., 1960). The role, if any, of built-in avoidance seems then to be at the most rather limited. Even a slight hesitation to attack,

however, may be of some importance in terms of evolution.

A further possibility can be derived from examination of the work of Coppinger (1969, 1970), who was able to show that novel food items could elicit avoidance independently of their coloration. The effects of "novelty" or "strangeness" in decreasing the frequency of attack (at least under laboratory conditions) have been since confirmed (Shettleworth, 1972).

Studies of the effect of the mimic on rates of predation of the model are mostly of a speculative nature since the attention of experimenters has usually been focused on the reverse effect (model upon mimic). It is theorized (see Fisher, 1930) that the presence of mimics is a factor in promoting an increase in the conspicuousness ("distinctiveness") of the models. Nur's theoretical analysis (1970) suggests a faster evolution of the mimic toward the model than of the model away from the mimic (see the concept of "advergence" proposed by Brower and Brower, 1972).

An exception to the seemingly general lack of experimental interest on the effects of mimics on the model is represented by Lea and Turner's paper entitled ".... The Effects of a Batesian Mimic on its Model" (1972). The authors' conclusions seem to support Fisher's hypothesis. They recognize, however, weaknesses in the design, originally intended for a study of Müllerian mimicry, and

suggest other possible interpretations of their results. Basic information in this respect appears, therefore, to be still largely missing.

c) Mimic

Mimetic advantage was first recognized by Bates in 1862, but for a long time experimental evidence remained essentially lacking. A great deal of attention has, however, since been given to the problem, following the brilliant series of the Browers' studies in the late 1950's (e.g., Brower 1958 a,b,c). The hypothesis that Batesian mimetic coloration is protective appears today to have been demonstrated beyond doubt. Extensive summaries are available in the literature (e.g., Carpenter and Ford (1933) and Cott (1940) for early work, Wickler (op.cit.) and Rettenmeyer (op.cit.) for more recent reviews).

The initial steps of mimetic resemblance have been also investigated. It is theorized that the evolution from a non-mimetic form is due to small, continuous variation; even very imperfect mimics are hypothesized to have some advantage, and relatively more perfect ones to have greater and greater advantage.

The early experimental evidence appears to point towards corroboration of the hypothesis (e.g., Schmidt, 1960; Cook, 1969; Pilecki and O'Donald, 1971). In 1971,

however, Brower, et al., could still confidently state that "no one has yet conclusively demonstrated with a large sample of birds using a plausible incipient butterfly mimic that this mimic could derive an advantage from its colour pattern resemblance, albeit imperfect, to the model species" (p. 263). For instance, for a long time novelty effects were not considered in experimental designs, and some of the experiments done prior to Coppinger's (1969) work may be in need of critical reinterpretation. Later studies (e.g., Ford, 1971) have attemped to control for novelty, and seem to confirm the advantages gained by initial mimics over non-mimetic forms.

Recently Terhune's work (1976) and the present study have independently demonstrated the importance of still another previously overlooked experimental factor. Both studies have shown that some birds can, prior to tasting, differentiate between artificial mimics and models in the absence of experimentally presented differential cues. It appears that the discrimination is based on slight differences due to the embittering treatments of the artificial model. Conclusions from previous experiments, which had not controlled for this factor, could, therefore, be questioned.

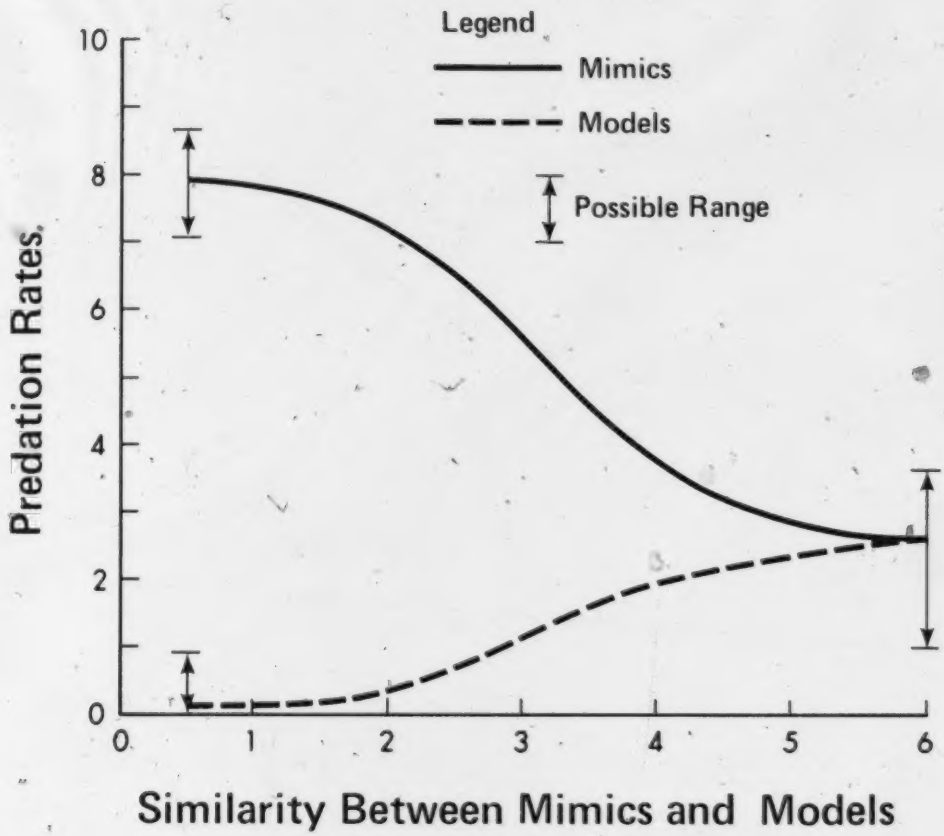
d) Mimic-model system

A system constituted by a mimic and its corresponding model is considered to be dynamic, both from an evolutionary standpoint (Ford, 1975), and from the standpoint of changes in the individual predator's experience (Holling, 1963). Regardless of relative numbers (Brower, 1960; Emlen, 1968), and time of appearance (Bobisud, pers. comm.), a major parameter in a mimic-model system is the degree of similarity between the pair.

A number of studies have used gradients of "mimetic resemblance" as the basis for speculations about hypothetical changes in the frequency of predatory attacks on the mimic forms (e.g., Sheppard, 1962). On the gradients different degrees of similarity are usually indicated in a qualitative way. Along these lines I have constructed an idealized model involving both components of a mimic-model system (Figure 1); the basic relations of this model are not mathematically defined, but derived from the following theoretical considerations.

The assumptions made are: a not-too-distasteful model (multi-trial learning); absence of color preferences; equal numbers of encounters of mimic and models; and independence of the degree of similarity from the particular characteristics of the two colors involved. With increasing

Figure 1. Hypothetical model representing changes in rates of predation with increasing similarity between pairs of models and corresponding mimics. Values on the X and Y axes are arbitrary; possible ranges are indicated whenever the precise nature of the relationship is uncertain.


Legend
Mimics
Models
Possible Range
Predation Rates
10
8
6
4
2
0
0
1
2
3
4
5
6
Similarity Between Mimics and Models

similarity between the mimic and the model forms, less and less of the former appear to be subjected to predatory attacks (Wickler, 1968), until they are completely indistinguishable and the frequency of attacks on the mimics is as low as the one of the models (Pough, et al., 1973: automimicry). The models would, on the other hand, be attacked more, as the mimic's appearance approaches a perfect similarity (Fisher, 1930, p. 148). This increase in attacks on the models would, however, be expected to be less dramatic than the mimics' decrease.

Based on signal detection theory and on experimental results, Duncan and Sheppard (1965) suggested a sigmoid relationship between increases in similarity and mimetic protection (see also Oaten, et al., 1975). Such an hypothesis has been incorporated into Figure 1, and expanded to include a similar relationship with respect to the model. Non-linear effects of changes in stimulus intensity over frequency of responses are often demonstrated, and linear relationships appear to be rather exceptional than the rule.

In experimental work, with methods using food coloring (e.g., Terhune, 1976) or paint (e.g., Sternburg, et al., 1977) to obtain artificial mimics and models, the degrees of similarity are subjectively assessed. Terms such as "initial" or "good" mimicry are widely used without any precise definition. The term "poor mimicry" has for instance

been applied to such diverse situations as a yellow edible prey mimicking a red model (Morrell and Turner, 1970) or a "reddish purple" prey mimicking a totally blue model (Ford, 1971).

2. METHODS

A laboratory study of mimicry involves a number of simplifying assumptions, which limit the possibility of generalizing its results to a complex natural system. However, it is generally felt that the advantages of such an approach, and the mass of information that it can yield, greatly outweigh the disadvantages of the unnaturalness of the conditions. Thus, I did not attempt to closely simulate "natural" conditions; instead I studied the properties of an artificial model with fixed or controlled conditions. In setting up such a model, I took a number of arbitrary decisions that will be detailed and discussed with the relevant methodological details. However, I feel that the general characteristics of a predator-mimic-model system have been retained. Of those listed by Rettenmeyer (op.cit., see p. 1), only (c) was not present in my experimental design.

Use of the terms "predator", "prey" and "attack" in reference to my experimental conditions (quail and seeds) has been based on the following considerations. First, seeds of many infesting weeds appear to have become mimics of seeds of cultivated plants; similarly other mimetic traits of plants have been described (reviewed by Wickler, 1968). Second, similar terminology has been frequently employed in the recent literature in reference to similar situations

(e.g., Morrell and Turner, 1970; Manly, et al., 1972).

Following a preliminary experiment, three major experiments (A, B and C) were run successively during this study. Experiments A and B constituted the main body to which the methods described below refer, unless otherwise specified.

2.1. Aims

In the present study I attempted to assess the effects, on the frequency of predatory attacks, of different degrees of similarity between a not-too-noxious model (multi-trial learning) and its mimic. For this purpose I examined various artificial predator-mimic-model systems, in an hypothetical progression to better mimicry, testing for significant decrements or increments in frequency of attacks on the models and on the mimics.

During Experiment A, prior to testing for effects of mimetic similarity, I attempted to control for and, if possible, to determine separately the effects of other factors which, on the basis of the existing literature (reviewed in chapter 1), I expected to make contributions to the overall effect. The ones I took into consideration were: novelty and its decrease over time; coloration per se; learning over time; and introduction of unpalatability. During the course of this experiment, it became clear that

good discrimination abilities had also an important effect. The implementation of a different design in Experiment C was an attempt to overcome such abilities on the part of the experimental animals.

On the basis of the results of Experiment A, Experiment B was planned with the aim of refining the study of good discrimination abilities. It also provided information about the carry-over effects of novelty superimposed on the mimetic effects.

2.2. Design

A similar design , implementing a number of well-known techniques of mimicry studies, was used with slight modifications for both experiments A and B. The following paragraphs outline it; details will follow.

In each experiment a group of caged birds was used to simulate predation, each individual bird being repeatedly tested throughout each experiment (repeated measurements design), each treatment representing a progress over the previous one.

Each artificial "prey" item had an ingestable part (one seed of wheat) and a non-ingestable part (the contiguous colored substrate). The latter was intended to provide, by its coloration, cues associated with the "mimetic" or "warning" characteristics of the prey.

Distastefulness of a "model" prey was simulated by treating the wheat seeds with an embittering substance (unpalatable seeds). The "mimic" prey was represented by untreated seeds (edible seeds).

In order to explore different aspects of the experimental situations each experiment was divided, following an acclimatization period, into two successive phases, each subdivided into successive subphases. As a reference, I have numbered the phases in chronological order (1, first, and 2, second); the subphases with two digits, the first digit indicating the phase and the second the chronological order, within each phase, starting with 0 (e.g., Subphase 1.0 is the first subphase of Phase 1).

Initially, during Phase 1, the birds were only exposed to edible seeds; subsequently, during Phase 2, unpalatable seeds were used also. Thus, the mimic-model systems were only studied in the latter phase. The experiments differed somewhat in the duration and type of the tests made during each phase. Generally, within each phase a number of pairs of color substrates was tested, each over a period of two or more experimental sessions. Phase 1 was a preparatory stage to Phase 2; therefore, I will first describe the latter.

During Phase 2 different pairs of mimic and model prey (color/seed complex) were tested over time, in order of increasing mimetic resemblance. Thus, in every session of Phase 2 generally the edible seeds were associated with one

substrate color of a pair (mimic) and the unpalatable seeds with the other (model). This association was never reversed for the same bird and within the same color pair. Which color became the mimic and which the model, for every color pair tested, was considered irrelevant, since the amount of "mimetic resemblance" changed only between color pairs, not within.

During Phase 1, to control for, and/or to assess, novelty effects and possible color preferences, the same colors and color pairs to be tested during Phase 2 were presented only with edible seeds. Thus, no punishment was present during Phase 1; in this phase the novelty effects, if any, could not be contaminated by effects of change of reinforcement schedule (positive *vs.* positive/negative).

In the two experiments various other aspects, to be detailed later, were superimposed on this basic design, to take into account other experimentally relevant factors, such as seed/background contrast, introduction of punishment, *etc*.

My basic measurement was, throughout the experiments, number of seeds pecked over the number of seeds presented. This constituted my dependent variable, while the other experimental treatments were the independent controlled ones (*e.g.*, color of substrates and their combinations; degree of food deprivation; prior experiences; schedule of reinforcement; ratio of edible/unpalatable seeds;

intersession intervals; and novelty).

2.3. Predators

Japanese quail (Coturnix coturnix japonica) were chosen as predators because of the possibility of raising them in captivity on a year-round basis, and their small size and limited maintenance requirements seemed ideal. This species may not be considered an important natural predator of any mimicry system. However, it occasionally feeds on insects, and it is known to possess the basic characteristics of such predators - the generalization of aversion to different colors (Czaplicki, et al., 1976), and learning abilities (Meinecke, 1974). For this reason, and in the light of the positive factors previously noted, I felt its implementation in this study was justified.

In an attempt to minimize the possible variability due to sex and previous experience, I used only sexually mature females that had been raised together from hatching. Horter and Ducker (1976) found that the learning ability of Japanese quail varies with age, levelling off shortly before sexual maturity. Consequently the experiments were started with individuals 12 weeks old.

Generally ten quail were utilized in each experiment, being tested throughout. Two weeks prior to the start of the experiment, the ten quail were moved to individual cages in

an observation room (acclimatization period). These individual cages (18x20x25 cm high) had three metal sides, and three wire mesh sides in the front, rear and bottom. Individual water and food dishes were provided outside an opening cut into the mesh of the front of the cage. The solid lateral walls prevented adjacent animals from seeing each other most of the time.

Outside the experimental sessions, the animals were fed a standard food for laboratory birds, Turkey Starter.

2.4. Prey

The most frequently utilized prey types in experimental mimicry studies are: dead butterflies, pastry rolls and mealworms. The first two alternatives were rejected, after consideration of availability and of time factors; the last one could only be consumed in small amounts, and I felt that a large sample size was preferable. I therefore adopted a fourth alternative, wheat seeds, since they appeared to possess a number of desirable qualities, such as: unlimited availability at any time of the year; discrete units of relatively small size; ease of storage and maintenance; and compatibility with the dietary requirements of the experimental species.

Two characteristics of the prey are usually experimentally controlled in this type of mimicry study:

a) palatability and b) coloration. The other features (smell, shape, nutritional value, etc.) are not usually manipulated, and I attempted either to keep them constant or randomly variable. Such attempts, as will be seen in the results, might not have proven fully successful.

a) Taste type.

Two palatability types of prey were considered: edible and unpalatable. These categories are necessarily arbitrary, but can be defined in terms of the food items (wheat seeds) and of the experimental treatment(s).

For the unpalatable seeds I used the treatment most often reported in literature, a 60% solution of quinine dihydrochloride monohydrate. The seeds were soaked for 24 hrs in the solution, dried at room temperature for 24 hrs and stored in the dark for about 48 hrs prior to use. The same treatment was applied as a control to the edible seeds, but only water was used.

b) Coloration.

With respect to coloration, two basic procedures had been used in previous studies: coloring of the prey, and coloring of the prey's substrate. In an effort to standardize conditions, I adopted the second strategy. This eliminated the prey's own color variability. Furthermore,

I felt that I could obtain better results by exposing the birds to the mimetic (substrate) cues for longer periods of time, including prey ingestion time. Pieces of uniformly colored paper (20x20 mm) were used as substrates.

The experimental colors were chosen in an attempt to represent some of various "mimetic resemblance" degrees, subjectively assessed. The rationale behind these choices will be explained in chapter 2.6.e, when describing the experimental phasing. In an attempt to objectively define the colors, both those of the substrates and those of the two seed types, I have matched each color with the color samples provided by the ICI Colour Atlas (Table 1). The reference system of the atlas is based on four coordinates, of which three are read to uniquely define each color sample.

2.5. Prey presentation

a) Presentation apparatus

A modification of the apparatus used by Schuler (1974) was used for successive presentation of the seeds. Thirty-seven plastic trays (4x4x.5 cm deep) bordered a horizontal revolving wheel (55 cm in diameter) mounted on a wooden frame (Figure 2). The trays were hidden from the birds' sight by a cardboard screen, which only presented a

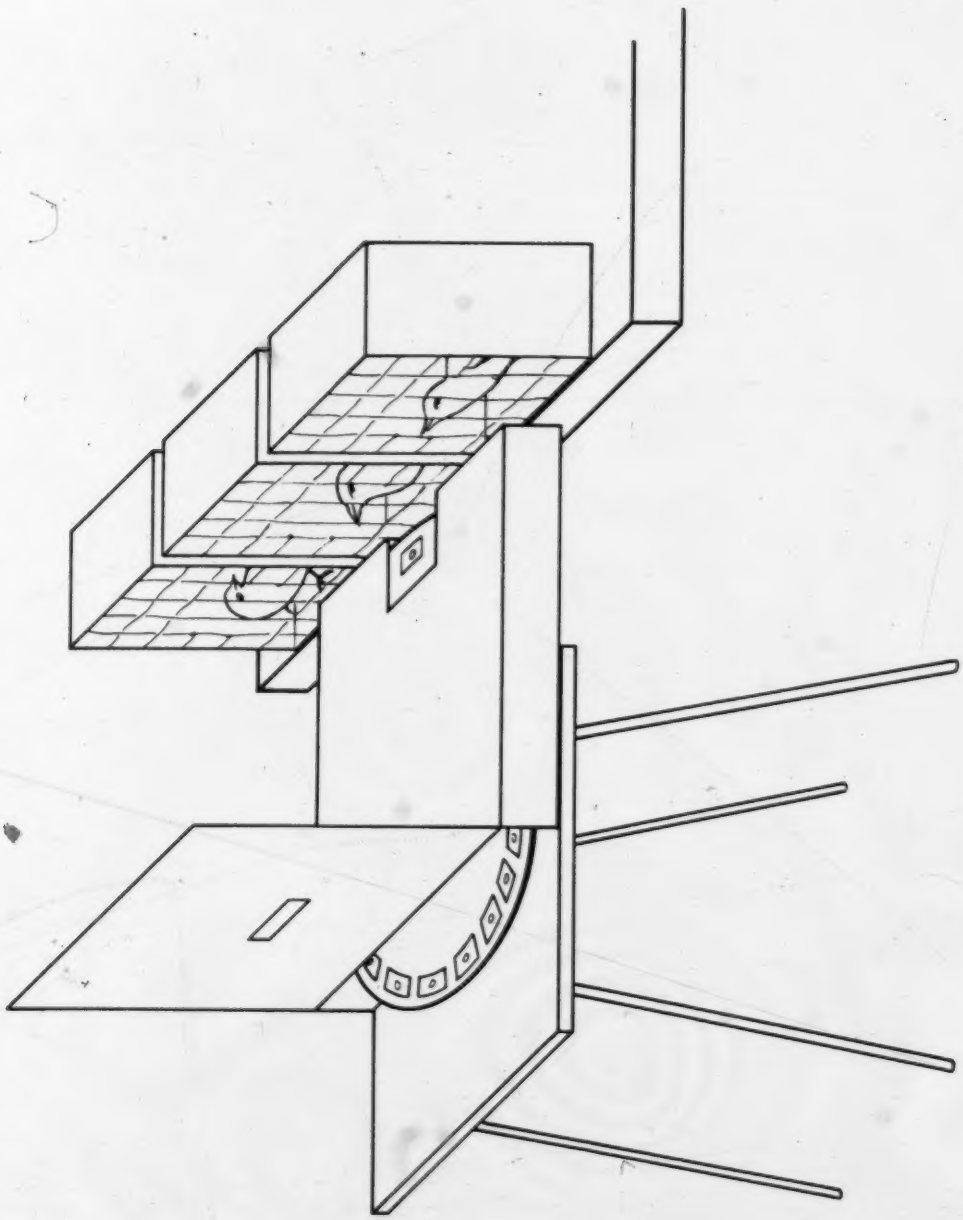
Table 1. Classification of color substrates and seed colors according to the ICI Colour Atlas.* Each color is indicated, in the first column, with the description name used in the text.

Color Name	Y	R	B	N
White	1	1		3
Red	7	17		1
Orange	9	15		2
Green	5		9	2
Blue 1	0		5	2
Blue 2	1		12	10
Brown 1	5	7		8
Brown 2	4	7		10
Violet 1		15	6	4
Violet 2		9	5	1
SEEDS edible	7	9		11
SEEDS unpalatable	8	9		11

Y, R, B, N: ICI Colour Atlas coordinates.

* - Imperial Chemical Industries, Ltd. 1971. ICI Colour Atlas. London, Butterworths.

Figure 2. Apparatus for prey presentation utilized in the experiments A and B. In the diagram cages and apparatus are shown in their respective positions during an experimental session.



frontal rectangular opening (5x8 cm). By rotating the wheel, one tray at a time could be exposed through the opening of the screen (successive presentation design). The rotation was such that each tray was at least partially visible for a total of about 6 seconds; for two thirds of this time, the tray was completely exposed and motionless.

Each tray was lined with a piece of the colored substrate; whenever seeds were used, one seed was placed approximately in the centre. As a general rule, during every session each experimental animal was presented with a total of 148 trays over approximately 15 minutes. This presentation of 148 trays will be called one trial.

In an attempt to minimize density-dependent effects (such as search image formation and apostatic selection), I maintained at about the same levels the proportions of each type of prey tested (generally 72:76). The sequence of presentation was randomized.

b) Regime

The photoperiod was kept constantly at 12D/12 L. The daily experimental sessions started at 3 p.m., after six hours of light. Four hours of food deprivation were arbitrarily decided to precede each daily session: standard food was available ad libitum from 7 p.m. to 11 a.m.; water was available at all times except during each trial.

To minimize disturbance each bird was tested in its cage, which was not moved from its usual location. At the start of each trial, the presentation apparatus was positioned so as to allow the bird under observation to see and reach the successively exposed trays. An experimental session included one trial per bird, randomly assigned to one of ten starting times, at 20 minute intervals, beginning at 3 p.m.. The session ended at 6.20 p.m. For reason of sickness, disturbance, etc., in a few cases not all the birds could be tested during each session.

2.6. Phases of experiments A and B

The experimental plans for experiments A and B are presented, with the exception of the acclimatization period, in Tables 2 and 3. The tables indicate the primary characteristics of each phase and subphase, its length, the colors and types of seeds used and the major differences, whenever applicable, of treatment of birds in the same experiment.

In the following paragraphs the phasing of each experiment will be detailed.

a) Acclimatization period

When 12 weeks old, the ten quail were separated and moved to individual cages in the experimental room. The next

Table 2. Experimental plan for experiment A (see text). The birds from # 1 to 10 have been tested throughout this experiment, with the exceptions indicated.

Phase #	Subphase #	Color pair #	Color	Session #	Number of Birds Tested[c]
	1.0 Pre-training (only one color substrate)	1st	White	1st 2nd 3rd 4th 5th 6th 7th	10 10 10 10 10 10 10
1. Edible seeds only	1.1 (pairs of color substrates)	1st (sub-subphase 1.1a)[a]	Red/Blue 1 (+Brown 1)	1st 2nd 3rd 4th	10 10 10 5
		2nd	Orange/Green	1st 2nd 3rd	10 10 5
		3rd	Blue 2/Brown 2	1st 2nd	10 10
		4th	Violet 1/Violet 2	1st 2nd	10 10
	2.0 Conditioning (pairs of color substrates)	1st	Orange*/Green	1st 2nd 3rd 4th 5th	10 10 10 7 7
2. Edible and unpalatable seeds	2.1[b] (pairs of color substrates)	1st	Brown 2*/Blue 2 (subgroup A) or Brown 2/Blue 2* (subgroup B)	1st 2nd	10 10
		2nd	Violet 1*/Violet 2 (subgroup A) or Violet 1/Violet 2* (subgroup B)	1st 2nd 3rd	10 10 10
	2.2 (only one color substrate)	1st	White*/White	1st	10

[a] - in this sub-subphase, the color Brown 1 was present without seeds until the 3rd session, and partially with seeds during the 4th session (see text).

[b] - in subphase 2.1, the birds have been divided into subgroup A (#1 to 5) and subgroup B (#6 to 10).

[c] - birds tested for the number of sessions indicated within each color pair.

* - color associated with the unpalatable seeds.

Table 3. Experimental plan for experiment B (see text). The birds from # 11 to 20 have been tested throughout this experiment, with the exceptions indicated.

Phase #	Subphase #	Color pair #	Color	Session #	Number of Birds Tested[a]
	1.0 Pre-training (only one color substrate)	1st	White	1st 2nd 3rd	10 10 10
1. Edible seeds only	1.1 (pairs of color substrates)	1st	Blue 2/Brown 2	1st 2nd 3rd	10 10 8
		2nd	Orange/Green	1st 2nd	10 10
2. Edible and unpalatable seeds	2.0 Conditioning (pairs of color substrates)	1st	Orange/Green*	1st 2nd 3rd 4th 5th	10 10 10 9 4
	2.1 (pairs of color substrates)	1st	Brown 2*/Blue 2	1st 2nd 3rd 4th	10 10 10 10
	2.2 (only one color substrate)	1st	White*/White	1st 2nd	10 8

[a] - birds tested for the number of sessions indicated within each color pair

* - color associated with the unpalatable seeds.

two weeks were used as an acclimatization period - to the light regime, isolation, new cages, different environment and the presence of the experimenter. During this period no test was conducted with this group of animals. However, at the same time in the same room an experiment was, whenever possible, run with a different set of quail. The first group was prevented from direct observation of the test being performed, but it could see most of the experimenter's movements and hear all noises.

b) Phase 1: Edible prey only

During Phase 1, the colors and color pairs, to be used in the succeeding Phase 2, were tested in association only with edible seeds.

The aim of this phase was basically threefold: 1) to provide for a test of color preferences in the absence of unpalatable seeds; 2) to minimize and/or to evaluate the effects of "novelty" on the results of Phase 2; 3) to measure, as a control, the frequency of attack on edible seeds in the absence of unpalatable ones.

Phase 1 was sudivided into Subphase 1.0 (pre-training), aimed at training the animals to eat edible wheat seeds from the apparatus for prey presentation; and Subphase 1.1 (main testing period), where various sets of two colors were used as substrates.

In Experiment A, in an attempt to eliminate most of the possible variance due to novelty effects, I subjected the birds to a prolonged Phase 1. In order to detect possible effects of seed/ground contrast, I also included in this experiment a Subphase 1.1a at the beginning of Subphase 1.1. Details on the methodology used during Subphase 1.1a will be given with the results.

In Experiment B I attempted to see whether or not reduced amounts of previous exposure would have any decremental effects on pecking frequencies. For this reason Phase 1 of Experiment B involved fewer sessions and fewer color pairs than Phase 1 of Experiment A.

c) Subphase 1.0: Pre-training

In Experiment A the pre-training period was arbitrarily chosen to encompass a week (sessions 1 to 7). In Experiment B this period was shortened to 3 days (sessions 1 to 3).

The color associated with the seeds in this subphase was white for both experiments. A daily pre-training session lasted 15 minutes, regardless of number of seeds attacked. During the initial first pre-training session many seeds (about 15) were presented together on the same motionless tray. By slow motion successive new trays with a variable number of seeds (from 15 to 1) were uncovered. With time

fewer seeds were put in the same trays. By the end of the first session, each tray contained only one seed and was moving at the standard speed.

During the whole pre-training period of Experiment B, and until the sixth day of Experiment A, no quantitative data but only qualitative accounts of the birds' behavior toward the seeds and the apparatus were recorded. Initially frequent escape attempts, freezing, some alarm calls, and general sign of distress were recorded for almost every bird. In two or three days such manifestations subsided and all animals, by this time, ate the seeds with apparent eagerness.

d) Subphase 1.1: Color-pairs/edible-seeds association.

In Experiment A four sets of two colors - red and light blue (Red/Blue 1), orange and green (Orange/Green), dark brown and dark blue (Brown 2/Blue 2), dark violet and light violet (Violet 1/Violet 2) - were used as substrates for the edible seeds in a number of successive sessions. In Experiment B two of the previous pairs were used: Brown 2/Blue 2 and Orange/Green.

e) Phase 2: Mimic-model systems

The present phase was designed to test the quails' reactions to different mimic-model systems, involving

various degrees of "mimetic resemblance". Both edible and unpalatable seeds were presented in the same sessions; about half of the seeds presented in any given session were of either seed type, in association with either color (or with white).

In this phase, Subphase 2.0 was a conditioning period, which includes the first exposures to the unpalatable seeds. It can, therefore, be compared to Subphase 1.0 as a training period, this time designed to familiarize the animals with the presence of unpalatable seeds where previously only edible seeds had been offered. Subphase 2.1 and Subphase 2.2 were the main testing periods. The latter Subphase was originally designed to test the abilities of the subjects to discriminate the two types of seeds on the basis of treatment alone, prior to tasting and in absence of color cues.

Choice of the pairs of color substrates tested was based on the following considerations. Each individual color was selected in such a way that each successive color pair would represent a progression toward increasing mimic/model resemblance and at the same time be sufficiently distinct from the previous pair to avoid confusion in learning the successive steps. Thus, in Subphase 2.0 I tried to minimize possible effects of "mimetic" factors: in this subphase a supposedly "non-mimetic" color pair was used (Orange/Green). In Subphase 2.1, in an attempt to reduce the extent of

possible mimetic similarities across color pairs, I originally decided to test only two color pairs, i.e., a supposed "poor" mimetic pair (Blue 2/Brown 2) and a "good" one (Violet 1/Violet 2). I intended to avoid a "perfect" mimetic situation, which, by presenting a too difficult discrimination problem, may have caused experimental neurosis in my subjects. However, when I realized that the treatment of the seeds could be discriminated per se, Subphase 2.2 was added. In this subphase only one color substrate was used, the same for both seed types. I chose White, since it appeared distinctive from the previous pairs of Phase 2, and the birds had already been exposed to it in Phase 1. The effects of such discrimination on my subjective classification of mimetic resemblance will be discussed with the results.

f) Subphase 2.0: Conditioning

In Experiment A the unpalatable seeds were associated with the Orange substrate, while the edible seeds were presented on the Green substrate. In an attempt to also provide for some controls of different rates of learning for the two colors, if any, in Experiment B for all the birds the reverse association was maintained (Green with unpalatable seeds, Orange with edible).

g) Subphase 2.1: Color-pairs/seed-types association.

Experiment A Subphase 2.1 successively examined two different pairs, Blue 2/Brown 2 and Violet 1/Violet 2.

In order to try to assess the magnitude of possible "learning preferences", in this subphase the birds of Experiment A were subdivided into two subgroups of five animals each (A and B). The two subgroups were randomly assigned to either one of the two possible combinations of seed type and color. Subgroup A (birds 1 to 5) was presented with unpalatable seeds constantly associated with Brown 2 (or with Violet 2) and the edible seeds always with Blue 2 (or with Violet 1). Subgroup B (birds 6 to 10) was instead presented with the reverse combinations: Blue 2 (or Violet 1) as a substrate for the unpalatable seeds, and Brown 2 (or Violet 2) as a substrate for the edible ones.

In the same Subphase 2.1 of Experiment B, only one color pair and only one seed-type/color combination (i.e., Blue 2 with edible seeds and Brown 2 with unpalatable seeds) was tested for the totality of the experimental subjects.

h) Subphase 2.2: Same color substrate for both seed types.

The basic procedure of Phase 2 was maintained also during Subphase 2.2. Here only one color (white in both experiments) was used where previously there had been color pairs. The total number of seeds presented per session was

the same as it had been in the preceding subphases.

This subphase encompassed one session in Experiment A and two sessions in Experiment B.

2.7. Scoring system and data analysis

In Experiment A and B six categories of responses were quantitatively recorded. They were: (a) seed not touched; (b) seed pecked at and immediately lost; (c) seed rapidly tasted but almost immediately lost; (d) seed tasted thoroughly and rejected; (e) seed tasted thoroughly and swallowed; and (f) seed rapidly swallowed.

In a more natural situation an insect prey, even a "tough" model, could be seriously damaged if not killed by a predator's attack. The probable outcome would then be some loss of fitness, which is difficult, however, to properly assess. For this reason I decided to follow the most conservative analytical approach used in literature and grouped the six categories in "attacked" (b to f) and "not attacked" (a). The former category includes all the seeds touched in any way by the birds, regardless of the outcome.

The total numbers of seeds "presented" per color/seed complex were variable to a certain extent. In order to make the data more homogeneous, they were transformed prior to the analyses into percentages of seeds "attacked" out of the total "presented" in that complex. The transformed data were

considered to meet the assumptions of factorial or mixed model analysis of variance (ANOVA), which was the statistical test most used for data analysis.

Since the experimental design involved repeated measurements in successive treatments and non-randomized blocks, trend analysis of variance was utilized (Edwards, 1972, pp. 330-368). Thus each treatment's interaction with the subjects (TXS) was used as the error term for the treatment; the subjects were assimilated with a random effect, and the treatments with a fixed one. The same reasoning was extended to each interaction between treatments tested against its interaction with the subjects. On the contrary, the subjects and their interactions have been tested against the highest order interaction, with the assumption that this represents the major error. Thus, in Table 7 (p. 49), where B is the symbol for the birds, I have tested: the color pairs (P), against P x B; the substrate colors within color pairs (C/P), against C/P x B; the sessions (S), against S x B; the interaction between the color pairs and the sessions (P x S), against P x S x B; the interaction between the substrate colors within color pairs and the sessions (C/P x S), against C/P x S x B (highest order interaction term); the birds (B) and the following interactions (i.e. P x B; C/P x B; S x B; and P x S x B), each against C/P x S x B.

A number of different treatments have been tested in this study; I have attempted, in presenting the results, to maintain in different tables a homogeneous terminology, consistent with that of Table 7. The following symbols have been generally used to indicate significant levels of probability: *, $p<.05$; **, $p<.01$; ***, $p<.001$. In the case of missing data, ANOVA using weighted means were avoided and t-tests were generally used to provide supplementary evidence. Analysis of mean differences have been conducted using Duncan's New Multiple Range tests. When the latter test was applied to ANOVA interaction means, I used as degrees of freedom the numbers of unconfounded comparisons, as suggested by Cecchetti (1972).

In Experiment C, a further category was recorded: (g) key not pecked (seed remains unseen). For the purpose of analysis, (g) was lumped with (a) in the "not attacked" category, with the exception of Subphase 2.2, where (g) was disregarded and the category of "not attacked" included only (a). Since only four birds could be used throughout for this experiment, non-parametric statistical tests (chi square with Yates' correction) were used for these data, arranged in 2x2 contingency tables, including, for every bird/section, seeds attacked and not attacked for each color of the color pair tested.

2.8 Methods and results of the preliminary experiment

A preliminary experiment was conducted, over a period of eight days, to determine the level of daily consumption of edible seeds under two extreme conditions: when no other food was available at any time (quail subgroup B) and when contemporaneous ad libitum access to standard food was allowed (quail subgroup A). A third subgroup of quail (C) was assigned, as a control, to standard food only. Six quail for each subgroup were used throughout the experiment. With the exception of timing and methods of food presentation, the regime and the experimental conditions duplicated those described for Experiments A and B. In each of the preliminary experiment's session the food items being tested were presented from 10 a.m. to 5 p.m. (7 hrs). Outside the experimental sessions Turkey Starter was given ad libitum to the quail of subgroups A and C. Measures of food intake were determined on a daily basis by comparing the weight and/or numbers of food particles before and after the session.

The results of subgroup A clearly indicate that even in absence of constraints, with standard food easily accessible, considerable numbers of edible seeds were consumed (Table 4).

For subgroup B, which would presumably express a maximum level of consumption, an overall average of 440 seeds/bird/session was obtained (Table 5). Even though the

Table 4. Consumption of wheat seeds and Turkey Starter, when presented together to subgroup A of the preliminary experiment.

Session N	Bird #	Wheat Seeds (numbers consumed per session)							Turkey Starter (gr)						
		1	2	3	4	5	6	Avg.	1	2	3	4	5	6	Avg.
1		7	35	39	26	77	26	35	18.9	19.7	11.0	11.5	11.5	12.7	14.2
2		32	113	30	149	84	223	105	17.0	20.6	15.6	17.4	16.6	19.5	17.8
3		118	114	14	118	246	107	119	10.4	20.0	14.0	22.7	13.0	15.8	16.0
4		43	25	86	257	111	225	125	10.8	20.0	12.1	8.4	12.0	11.1	24.8
5		—	57	96	125	57	50	77	—	14.7	9.1	9.4	17.6	9.4	12.0
6		—	57	204	221	254	—	184	—	17.6	4.8	6.0	13.9	—	10.6
7		21	136	146	314	207	—	165	12.0	11.8	4.0	4.7	12.3	—	9.0
8		132	134	129	341	259	—	199	5.5	11.5	5.3	2.5	6.9	—	12.7
Avg.		59	84	93	194	162	126	122	24.9	17.0	9.5	10.3	13.0	13.7	12.6

Table. 5 . Consumption of wheat seeds and Turkey Starter, when presented alone to subgroups B and C in the preliminary experiment.

Session Number	Bird #	Wheat Seeds (Subgroup B) (numbers consumed per session)							Turkey Starter (gr) (Subgroup C)						
		7	8	9	10	11	12	Avg.	13	14	15	16	17	18	Avg.
1		285	346	257	119	222	128	226	15.0	13.7	10.3	16.5	5.3	12.5	12.2
2		429	404	470	247	501	276	388	23.5	18.0	18.7	17.0	11.2	16.5	17.5
3		493	529	786	430	643	329	535	27.5	18.8	22.0	17.5	15.6	12.0	18.9
4		477	428	432	440	485	375	440	23.0	16.3	21.8	14.4	14.4	26.4	19.4
5		524	407	382.	411	527	380	438	25.1	14.0	20.1	18.5	15.2	10.4	17.2
6		535	539	464	541	561	371	502	20.7	14.0	22.0	11.9	18.0	12.8	16.6
7		604	561	559	582	677	457	573	23.3	24.2	21.4	13.6	26.3	12.7	20.2
8		448	479	498	441	460	187	419	20.5	14.7	13.7	12.6	16.4	16.2	15.7
Avg.		474	462	481	401	510	313	440	22.3	16.7	18.8	15.2	15.3	14.9	17.2

experimental conditions of this preliminary experiment differ from those of the experiments A and B, these results give an indication of basic consumption of edible seeds.

3. RESULTS AND DISCUSSION

Mimetic resemblance between an unpalatable and an edible prey is only one of a number of factors that may, often unpredictably, affect frequencies of predatory attacks. In experimental studies of color mimicry, of necessity, many of these factors are present at the same time (e.g., "unpalatability", "learning" and "discrimination" abilities, "coloration", "hunger", etc.). Each factor may contribute in several different ways, varying with time, to the overall effect that is represented by the results obtained.

In an attempt to control for and/or to identify the relative contribution of these various dimensions, with each successive phase of the experiments A and B I progressively added complexity to the design. In Subphase 1.0 basic variables were present (i.e., edible seeds, hunger levels, presentation apparatus). Successively I added: "coloration" and "change" (novelty) of pairs of color substrates (during Subphase 1.1); "unpalatability" (during Subphase 2.0); and degrees of "mimetic resemblance" of pairs of color substrates (during Subphases 2.1 and 2.2).

In the following paragraphs, for the sake of analysis, I examine separately the possible contribution of each of the above listed factors to the overall effect, and whether or not their effects have stabilized before the introduction

of a new factor.

Unless otherwise specified, the following results refer to the experiments A and B, which have been discussed together for each factor considered. I have followed here, as much as possible, the chronology of the experimental phasing: extension over time of the expected effects of each factor, however, often prevented a closer correspondence to the progression of the experiments.

3.1. COLORATION PER SE

The possible contribution of coloration per se has been examined from two standpoints: "cryptic" value of seed/ground contrast and innate or early learned color preferences and/or avoidances.

a) Seed/ground contrast.

The color of the background was first considered, in Subphase 1.1a of Experiment A, from the standpoint of its possible "contrast" qualities (crypsis) with respect to the seeds, which may affect results independently of color preferences (Turner, 1961).

A light brown paper that appeared to approximate closely the color of the wheat seeds was chosen to represent the most "cryptic" background (Brown 1). After the pre-training period, in Experiment A, the presentation trays

were randomly assigned to Brown 1, Red and Blue 1 in the arbitrary proportions, respectively, of 17:10:10. For three consecutive sessions the birds were presented with no seeds on the Brown 1 paper, and edible seeds on the other two colors. The subjects appeared to associate absence of food rapidly with Brown 1 and, after the first one or two sessions, only rarely pecked at the empty (Brown 1) trays.

In order to test for possible crypsis of the seeds, and to assess the importance of "contrast", a fourth session was run with edible seeds being associated with some of the Brown 1 backgrounds. Red, Blue 1, Brown 1, Brown 1 without seeds, were arbitrarily assigned in the proportions of 6:6:6:17 respectively. The results indicate that, in the conditions of the test, presence of the most "cryptic" background failed to protect the seeds any more than did the more highly contrasting colors (Table 6). Pecking "habit" could be considered as a minor factor, if at all, since the empty trays, containing only the brown paper, were still very seldom pecked.

Lack of crypsis effects might be due to the detection by the birds of shadows (stereoscopic vision) or of seed/background color differences. Furthermore, the attention of the subjects had been focused upon the trays, and thus upon the location of the seeds, by previous locality training. In a more natural situation, on the other hand, it has been shown that much of the "cryptic" effect

Table 6. Comparison of attacks on edible seeds when associated in the same session with three substrate colors of different contrast value (Red, Blue 1, Brown 1). The analysis has been performed on data collected during the fourth session of the color pair Red/Blue 1 in subphase 1.1a of experiment A.

Source of variation	df	MS
Substrate Color (C)	2	.00104
Birds (B)	4	.12868***
C x B	8	.00321

derives from an "overlooking" of the prey by the predator (see Robinson, 1969, for a review), possibly due to a superabundance of background inedible objects with which the edible cryptic prey can be confused (de Ruiter, 1952) and/or to an unpredictable location of the prey.

Whatever the explanation, it appears that under these experimental conditions "blending" of the seeds with the background color could be disregarded as a significant factor affecting pecking rates.

b) Color preferences and/or avoidances.

As seen in the first chapter, the question of presence or absence of built-in differential responses to colors is still largely unresolved. In naive Japanese quail chicks Kovach (1974) found indications of preferences for some ambient light colors. Furthermore, even if my subjects were experimentally "naive", they may have developed learned preferences for some colors during the rearing period. For instance, Rabinowitch (1968) describes his naive hand-raised gull chicks as preferring, when tested, the food they had been used to, and its coloration, over different and differently colored food. For this reason, Subphase 1.1 of each experiment was analyzed for differences in attacks between the different colors.

The results failed to show differential reactions toward any of the colors (Table 7). On the contrary, the means of the seeds attacked in every session of this subphase appear to be very close for the two colors of the pair tested (Figures 3 and 4). Similar negative results are obtained also when comparing between experiments the same colors and color pairs (Table 8).

Color preference may, however, only be evidenced in particular contexts. Consequently, I also felt it necessary to provide for some control of color preferences in the presence of unpalatable seeds. During Subphase 2.1 of Experiment A, the birds were divided into two subgroups and randomly assigned to one or the other of the two possible color/seed-type combinations for every color pair (Blue 2/Brown 2 and Violet 1/Violet 2). There is no evidence of differences due to whichever color of each color pair was associated with unpalatable seeds (Table 9).

Within the Green/Orange pair of Subphase 2.0, which was not directly involved in my study of mimetic resemblance, orange was assigned to unpalatable seeds in Experiment A and to edible in Experiment B. In this subphase, a significant difference was detected between the two experiments (Table 10). As Table 11 shows, this significant difference was between edible seeds only, while attacks on the unpalatable seeds were not significantly different. Furthermore, the frequency of attacks of edible

Table 7. Comparison of attacks on edible seeds with different color substrates. The analysis has been performed on the first and second sessions for all the pairs of color substrates tested during subphase 1.1 in experiment A and in experiment B.

Source of variation	Experiment A		Experiment B	
	df	MS	df	MS
Color Pair (P)	3	.03738	1	.12036
Substrate Color/Color Pair (C/P)	4	.00405	2	.00456
Sessions (S)	1	.45338 *	1	.03005
P x S	3	.04271	1	.00044
C/P x S	4	.00657	2	.00138
Birds (B)	9	.06192***	9	.23659***
P x B	27	.04097***	9	.03023***
C/P x B	36	.00302	18	.00215
S x B	9	.05173***	9	.09885***
P x S x B	27	.03507***	9	.05735***
C/P x S x B	36	.00316	18	.00304

Figure 3. Means and standard errors for Phase 1 of Experiment A. The successive sessions of each color pair and subphase are shown in chronological order.

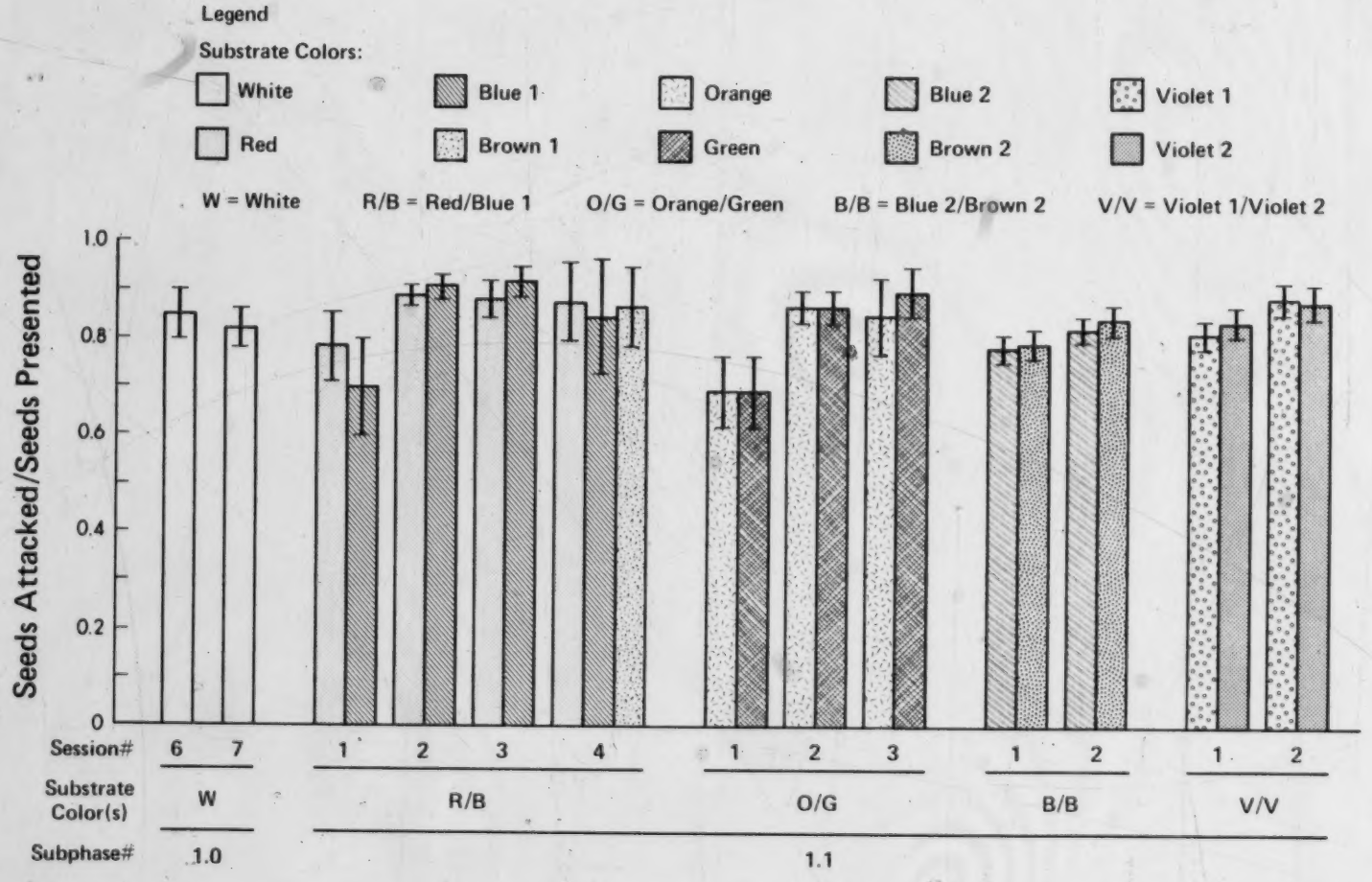

Legend
Substrate Colors:
White
Red
Blue 1
Brown 1
Orange
Green
Blue 2
Brown 2
Violet 1
Violet 2
W = White
R/B = Red/Blue 1
O/G = Orange/Green
B/B = Blue 2/Brown 2
V/V = Violet 1/Violet 2
Seeds Attacked/Seeds Presented
1.0
0.8
0.6
0.4
0.2
0
Session#
6 7
1 2 3 4
1 2 3
1 2
1 2
Substrate Color(s)
W
R/B
O/G
B/B
V/V
Subphase#
1.0
1.1

Figure 4. Means and standard errors for Phase 1 of Experiment B. The successive sessions of each color pair are shown in chronological order for Subphase 1.1.

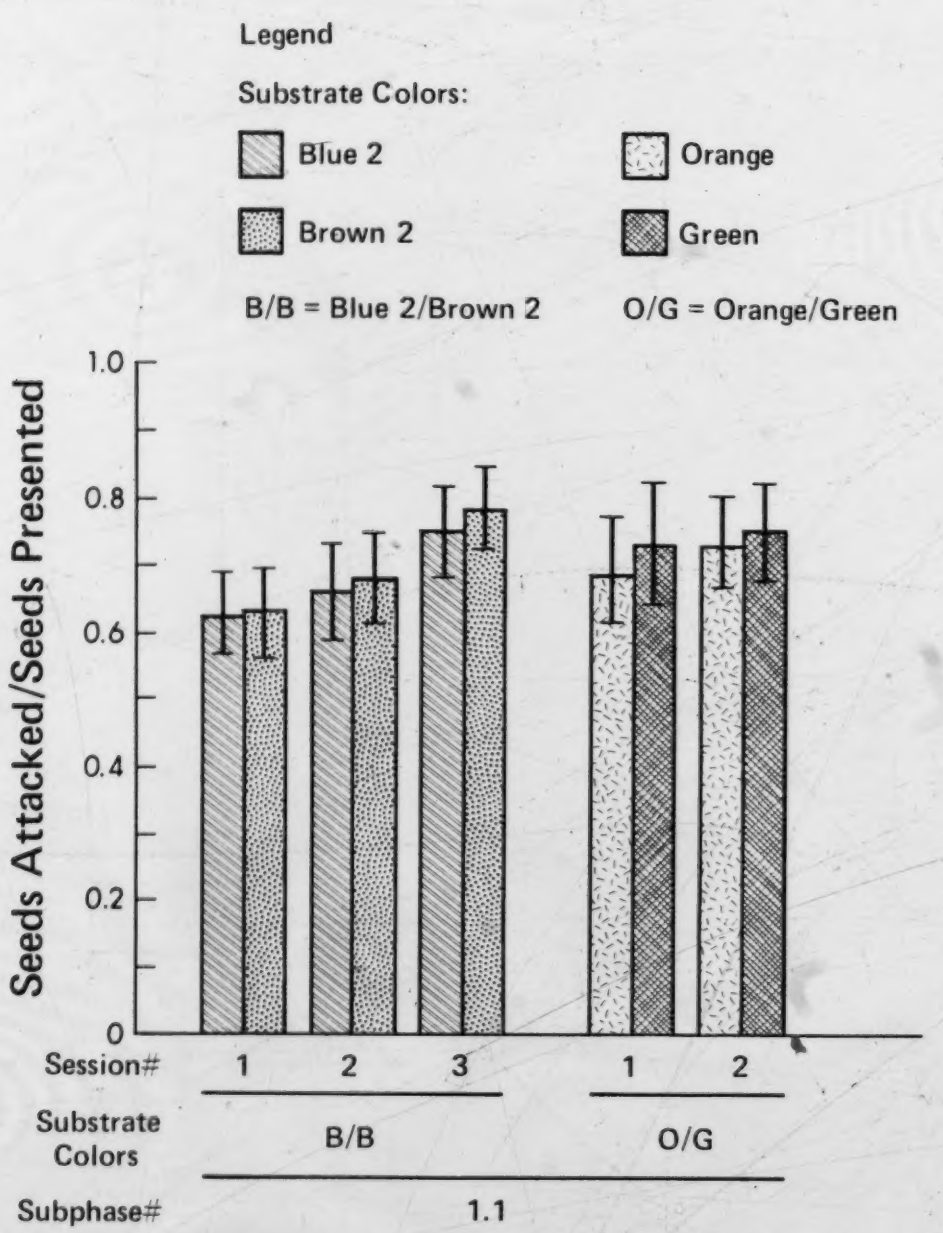

Legend
Substrate Colors:
Blue 2
Orange
Brown 2
Green
B/B = Blue 2/Brown 2
O/G = Orange/Green
Seeds Attacked/Seeds Presented
1.0
0.8
0.6
0.4
0.2
0
Session#
1
2
3
1
2
Substrate Colors
B/B
O/G
Subphase#
1.1

Table 8. Comparison between experiments A and B of attacks on edible seeds when, during subphase T.1, associated with the same color substrates for both experiments. The analysis includes the first two sessions of the color pairs Orange/Green and Blue 2/Brown 2.

Source of variation	df	MS
Experiments (E)	1	.46555
Birds/Experiments (B/E)	18	.13767***
Sessions (S)	1	.21136
E x S	1	.04605
Color Pairs (Pc)[a]	1	.02354
E x Pc	1	.11372
S x Pc	1	.03346
E x S x Pc	1	.04521
Color substrates/Color pairs (C/Pc)	2	.0037
E x C/Pc	2	.00215
S x C/Pc	2	.00096
E x S x C/Pc	2	.0006
S x B/E	18	.06643***
Pc x B/E	18	.03772***
S x Pc x B/E	18	.04915***
C x B/Pc/E	36	.00137
S x C x B/Pc/E	36	.00254

[a] - In other tables, where Color Pairs indicated consecutive pairs, the symbol (P) has been used.

Table 9. Comparison between attacks on edible and unpalatable seeds when in association with one or the other color of a given color pair (see text). The analysis includes all the sessions held for the color pairs (Blue 2/Brown 2 and Violet 1/Violet 2) of subphase 2.1 of experiment A. Due to the structure of the data the analysis has been divided in two parts, one of which (2) includes the error terms for the other (1).

Source of variation	Blue 2/Brown 2		Violet 1/Violet 2	
	df	MS	df	MS
Part 1				
Substrate Color (C)[a]	1	.02663	1	.02679
Seed Type (T)[a]	1	3.51888***	1	3.21426***
C x T[a]	1	.02656	1	.20859
Session (S)[b]	1	.00227	2	.01361
C x S[b]	1	.01835	2	.01455
T x S[b]	1	.02686	2	.00176
C x T x S[b]	1	.0031	2	.1424
Residual[c]	32	.02636	48	.04907
Part 2				
Color & Seed Complex (Co)[c]	1	.02656	1	.20359
Birds/Color & Seed Complex (B/Co)[c]	8	.05152	8	.05899
Sessions (S)[c]	1	.00227	2	.01361
S x B/Co[c]	8	.01693	16	.04447
Seed Type (T)[c]	1	3.51888	1	3.21426
Residual[c]	20	.01855	31	.04891

[a] - Tested against B/Co in Part 2

[b] - Tested against S x B/Co in Part 2

[c] - Not tested for significance

Table 10. Comparison between experiments A and B of edible and unpalatable seeds attacked in the first three sessions of subphase 2.0. In experiment A, Orange was associated with the unpalatable seeds, and Green with the edible; in experiment B, the reverse associations were maintained.

Source of variation	df	MS
Experiments (E)	1	.52148*
Birds/Experiments (B/E)	18	.09796***
Seed Types (T)	1	.88675***
E x T	1	.17833*
Sessions (s)	2	.22266**
E x S	2	.07821
T x S	2	.17527***
E x T x S	2	.00939
T x B/E	18	.02898*
S x B/E	36	.03938**
T x S x B/E	36	.01287

Table 11. Mean proportion of edible and unpalatable seeds attacked in the first three sessions of subphase 2.0, for experiments A and B (see table 10). N=30; standard error of the means = .031. The dotted lines separate means that have been found significantly different at the 0.05 level by a Duncan's New Multiple Range Test.

Experiment	Seed Type	
	Edible seed	Unpalatable seeds
A	.516	.267
B	.307	.212

seeds was significantly lower when associated with orange in Experiment B than when associated with green in Experiment A. The latter color is almost never considered a warning color, the former often (Cott, 1940). At first sight this finding might suggest avoidance based on warning effects of orange, in a system involving punishment, even if this is not contingent to the color being tested. However, on the basis of the following considerations I feel that the possibility of such an effect is unlikely.

Throughout this study, frequencies of attacks of edible seeds were consistently, though not always significantly, lower in Experiment B than in Experiment A. Such results, that will be presented and discussed in subsequent chapters, could not be, in most cases, attributed to color biases, since the same colors and color/seed-type combinations were then used for both experiments. On the contrary, they appear related to the difference in amount of previous experience that characterized the two experiments. In this light, a decreased attack frequency would be expected anyway in Subphase 2.0 of Experiment B, regardless of any other possible sources of decremental effects. Furthermore, in the remainder of this study color biases have never been demonstrated. Consequently, the present results could be explained just as well, or even better, with the present interpretation, since it had also been validated in other phases of this study.

In conclusion, if any in-born, early-learned, or differentially learned effects of coloration *per se* are present, they do not appear to be a major component affecting frequency of attacks on seeds under these experimental conditions. If at all present, they might be: (a) masked by the high variability found among the individual subjects; (b) too slight to affect the data significantly; (c) soon overcome by experience. A further alternative is that, regardless of color preferences, the colors are "ignored" as irrelevant to the situation (feeding). Such hypothesis seems, however, unlikely, since further examination of the results indicate that changing the colors of the background affects the rate of seeds attacked.

3.2. NOVELTY AND ITS DECREASE OVER TIME: PHASE 1

For a long time novelty of food items was assumed to elicit an increase in food intake, as confirmed in several experimental results (*e.g.*, Welker and King, 1962). It has also been shown, however, that such is not always the case, and that on the contrary, food novelty can be a powerful restraining factor (Coppinger, 1969; Shettleworth, 1972). In the light of these findings, some authors have tried to eliminate possible effects of "novelty" by pre-conditioning their experimental subjects to the prey prior to examination

of mimicry effects. However, the effectiveness of such methods is often only surmised.

I felt it was important to obtain information on this point and to examine the effects of successive introduction, in Subphase 1.1, of novel pairs of color substrates. For this reason, the Phases 1 of both experiments have been analyzed for changes over time between successive sessions. To allow for inclusion of Subphase 1.0 (where in one session only one color was used) and of Subphase 1.1a (where three colors were used) of Experiment A, and since the two colors of any pair had previously not been found to differ, I have analyzed the total proportion of seeds attacked per session regardless of the presence of different color backgrounds in the same session.

a) Experiment A: "Color" versus "change" novelty.

In the results of Experiment A there are clear indications of changes, with time, in the daily frequency of seeds attacked (Tables 12 and 13). Such changes appear to be related to the first session of exposure to a new color pair (see Table 7 and Figure 3).

Disregarding these first sessions, the mean values of seeds attacked in all the other sessions are consistent with each other and are very near to the total number of seeds presented (approximately 130 out of 148). Brief

Table 12. Comparison over experiments A and B, between all the sessions of phase 1 which have data for all ten birds (see text). For each bird all the data collected during each session on the different color substrates have been pooled.

Source of variation	Experiment A		Experiment B	
	df	MS	df	MS
Sessions (Sp)[a]	10	.05344**	3	.02505
Birds (B)	9	.02999	9	.11846**
Sp x B	90	.01996	27	.03105

[a] - Contrary to most other tables, where Session (S) has been used to indicate consecutive sessions in respect to color pairs, here the Sessions (Sp) are considered in respect to the whole phase 1.

Table 13. Means and standard errors of the proportions of seeds attacked by each bird in each session of experiment A pooled for the color substrates. Some data are missing from subphase 1.0. The dotted lines separate pairs of means that have been found significantly different at the 0.05 level. Duncan's New Multiple Range Test has been applied to the data analysed in table 12; for session where N is less than ten, t-tests have been used to compare contiguous pairs of means.

Subphase	Substrate Color (s)	Session Number	N	Mean ± SE
1.0	White	6th	10	.853±.058
		7th	10	.825±0.38
1.1	Red/Blue 1 (+ Brown 1)	1st	10	.742±.081
		2nd	10	.899±.022
		3rd	10	.900±.036
		4th	5	.869±.093
	Orange/Green	1st	10	.656±.074
		2nd	10	.864±.033
		3rd	5	.886±.068
	Blue 2/Brown 2	1st	10	.786±.023
		2nd	10	.830±.025
	Violet 1/Violet 2	1st	10	.825±.031
		2nd	10	.882±.033

interruptions in feeding may account for the failure to approach the 100 percent mark more closely. These birds thus appear to reach the levels of the consumption values obtained during the pilot experimentation (see Table 4). Thus, the lower values obtained during the first sessions of new color pairs appear to represent the decremental effects of "novelty".

During the second session of each color pair novelty effects appear reduced, since seed attacks regain the previous levels ("stability" levels). Furthermore, for the last color pairs the effects of novelty seem to wear off. This would appear to be true in respect to the first session as well since, following presentation of novel color pairs , only non-significant effects are shown. In the light of these results, it seems important to try to define more adequately what could constitute "novelty" in the present experiments.

On one hand, novelty effects might be caused by any colors never before encountered in a given situation ("color" novelty). Any new color pair would always be reacted to as a novel, fear-inducing stimulus regardless of how many changes in color had been previously experienced. At the same time any previously encountered colors, once habituated to, would not cause more novelty effects if re-encountered within the memory limits of the experimental subjects.

A different possibility is that novelty effects be due to the change in routine, regardless of which colors are actually involved ("change" novelty). Thus, reappearance of already encountered colors would have similar effects than introduction of completely new colors, since the "change" per se and not the "colors" would be the major novel factor present. Coppinger (1970) in examining the effects of novel butterflies on caged birds states that: "... what becomes evident here is that both the inhibition of attack and the strength of the response are a relationship between the amount of stimulus change and the past experience of the animals, and are not related to any particular characteristics of the stimulus per se" (p. 331). On the other hand, Menzel (1963) suggests that in young chimpanzees reared in isolation both changing and individual characteristics of the stimuli might have some effects on active avoidance. In my experiments, both novelty components (a generalized "change" novelty and a more specific "color" novelty) appear to affect seed-pecking rates synergetically and negatively.

b) Experiment B: "Apparatus" novelty.

The mean proportions of seeds attacked during Phase 1 of Experiment B are graphically represented in Figure 4. During Phase 1 of Experiment B, the decremental/incremental

pattern that was observed in Experiment A to be related with changes of color pair, is still present, even though differences are not significant (Table 12 and 14). The trend seems only more accentuated in Experiment A.

However, a comparison, involving the first and second pair of the two experiments, reveals that while the seeds appear similarly attacked during the first sessions for both experiments, such is not the case for the second sessions (Tables 15 and 16). Then, the levels of attack obtained in Experiment A ("stability" levels) are not reached in Experiment B.

It might be concluded that the "stability" levels of Experiment A would never be reached by this group of birds, independently of the experimental design. However, differences (Table 15) have been found over and above the birds' variations within experiments, and I feel that the sample size was large enough to reduce the probability of a chance clustering of low-variable birds in the same experiment. Furthermore, the frequency of seed attacks in the successive sessions of Phase 1 of Experiment B clearly shows a trend of almost continuous increase, indicating occurrence of some type of habituation (Figure 4).

As already pointed out, even though the level of seed attacks reached during the pre-training period of Experiment B is not known, there are clear indications that initially the pre-training sessions were a stressful experience for

Table 14. Means and standard errors of the proportion of seeds attacked by each bird in each session of subphase 1.1 of experiment B, pooled for the color substrates. No means were found significantly different. A New Duncan's Multiple Range Test has been used for the data analysed in table 12, experiment B. For the remaining session (3rd of Blue 2/Brown 2), t-tests have been used.

Subphase	Substrate Colors	Session Number	N	Mean ± SE.
1.1	Blue 2/Brown 2	1st	10	.626±.062
		2nd	10	.669±.066
		3rd	8	.768±.062
	Orange/Green	1st	10	.707±.091
		2nd	10	.742±.068

Table 15. Comparison between experiments A and B of attacks on edible seeds during the first and second sessions of the first two pairs of color substrates in subphase 1.1.

Source of variation	df	MS
Experiments (E)	1	.5186
Birds (B/E)	18	.15282***
Color Pairs (P)	1	.01336
E x P	1	.14067
Sessions (S)	1	.40589*
E x S	1	.15363
P x S	1	.00003
E x P x S	1	.00124
Color Substrates/Color Pairs/Experiment (C/P/E)	4	.00557
S x C/P/E	4	.00664
P x B/E	18	.05056***
S x B/E	18	.08956***
P x S x B/E	18	.05732***
C x B/P/E	36	.00362
S x C x B/P/E	36	.00371

Table 16. Mean proportions of edible seeds attacked during the first and second sessions, combined for the first two color pairs of subphase 1.1 in experiments A and B. N = 40; standard error of the means = .047. The dotted lines separate means that have been found significantly different at the 0.05 level by a Duncan's New Multiple Range Test (cfr. Table 15). In table 15, the E x S interaction had not been found significant, but the Duncan's Test was nevertheless performed for the reasons given by Edwards (1972, pp 130-131).

Experiment	Session	
	1st	2nd
Experiment A	.719	.881
Experiment B	.667	.706

every bird. Thus the presentation apparatus, when first experienced, seems to have constituted a "novelty" factor in itself, preventing the birds from eating at their full potential. The length of the habituation period to such "apparatus" novelty appears to be longer than the three days of pre-training in this experiment. In this case, the presence of an added novelty factor (the change of color background) interfering with an habituation process might explain the failure to reach "stability" levels in a time span comparable to that of Experiment A.

3.3. INTRODUCTION OF UNPALATABILITY: SUBPHASE 2.0

Subphase 2.0 included the very first presentations of unpalatable seeds (Figure 5). Therefore, I examined this subphase for possible effects of this change in schedule of reinforcement. A significantly lower frequency of attacks on the edible seeds was found when comparing, in each experiment, the first two sessions of this subphase to those of Phase 1 with the same type of seed on the same color substrates (Tables 17 and 18; see Figures 3 and 4). From the standpoint of mimetic resemblance, the colors of the background were considered as "non-mimetic". Consequently, no strictly defined mimicry effects could be considered as the cause of the observed decline in attacks.

Figure 5. Means and standard errors for Subphase 2.0. The upper graph refers to Experiment A; the lower to Experiment B. The successive sessions are shown in chronological order.

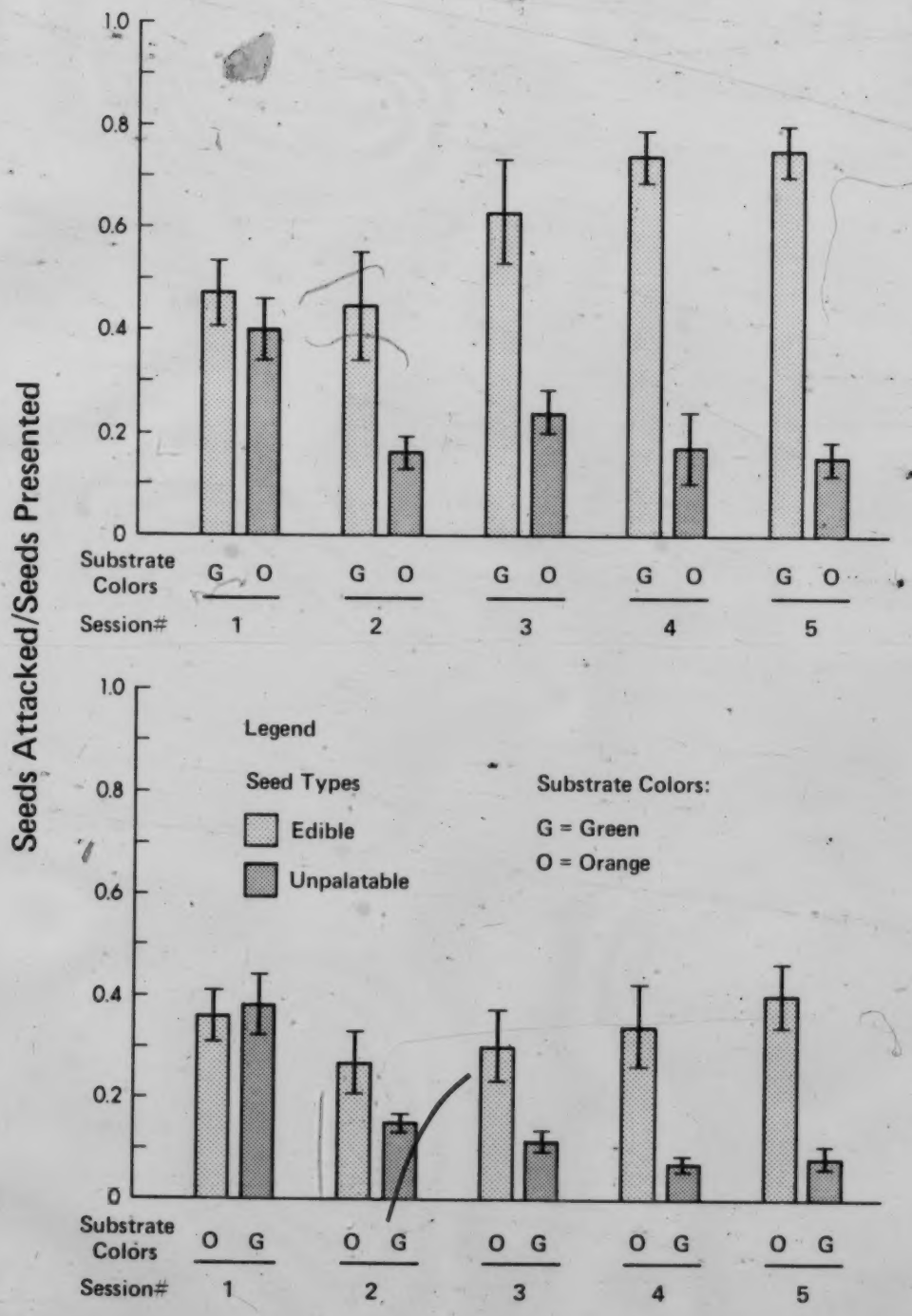

Seeds Attacked/Seeds Presented
1.0
0.8
0.6
0.4
0.2
0
Substrate Colors
G O G O G O G O G O
Session#
1 2 3 4 5
Legend
Seed Types
Edible
Unpalatable
Substrate Colors:
G = Green
O = Orange
1.0
0.8
0.6
0.4
0.2
0
Substrate Colors
O G O G O G O G O G
Session#
1 2 3 4 5

Table 17. Comparison between attacks on the edible seeds when associated with the same color (Green) in presence of unpalatable seed (subphase 2.0) and in their absence (subphase 1.1) in experiment A. The first two sessions of the color pair Green/ Orange are considered for each subphase.

Source of variation	df	MS
Phases: Presence of unpalatability (U)	1	1.02481***
Sessions (S)	1	.05149
U x S	1	.09633
Birds (B)	9	.08576
U x B	9	.05077
S x B	9	.04206
U x S x B	9	.03064

Table 18. Comparison between attacks on the edible seeds when associated with the same color (Orange) in presence of unpalatable seeds (subphase 2.0) and in their absence (subphase 1.1) in experiment B. The first two sessions of the color pair Orange/ Green are considered for each subphase.

Source of variation	df	MS
Phase: Presence of unpalatability (U)	1	1.58425***
Sessions (S)	1	.00636
U x S	1	.05462
Birds (B)	9	.10242**
U x B	9	.0392
S x B	9	.0392
U x S x B	9	.01776

Platt, et al., (1971) after training caged birds to "..eat a number of different species of brownish (palatable, N.o.E.) butterflies....as well as the...edible control butterfly....for the purpose of lessening novel stimulus effects..", state that, "Interestingly, all groups of birds showed a tendency to reject the controls during these trials following their initial unpleasant experiences with the unpalatable models." The authors do not, however, further elaborate on this finding. Other authors might have noticed similar effects; however, seldom have I found comments about the pre-conditioning periods in other mimicry studies.

I feel that two mechanisms, possibly acting synergetically, might be responsible for the results obtained in this study. The first involves the mimetic qualities of the two types of seeds, regardless of background color. The fact that the prey items utilized for the mimics and the models, and often the control, are basically the same does not appear to have been considered in itself as a mimetic factor in most experimental mimicry studies. I think it likely that in my experiment some of the great similarities between the two types of seeds may have had some sort of mimetic effects ("shape" mimicry).

Schideler (1973) in comparing frequencies of attacks against artificially painted mimic and model mealworms, demonstrated that even very small similarities of color/pattern are somewhat protective. It might be

speculated that in nature the generalized similarity of being "butterfly-like", even if colored in a completely different way from the distasteful butterflies, might constitute already a first step in mimetic resemblance. On the other hand, attacks on edible seeds during the first session of Subphase 2.0 appear to be lower than the ones obtained during Subphase 2.2, where the most perfect mimetic pair was tested. However, the difference is significant only for Experiment B (Table 19; see Figure 6, p. 94). Consequently, if this "shape" mimicry is a factor here, it would seem that either its effects wear off with time, or that some other factor(s) are also present.

The second possibility relates to the effects of the sudden introduction of unpalatable seeds after a long period when only edible seeds had been encountered (change in schedule of reinforcement). The simultaneous novel appearance of punishment, together with punishment itself, appears sufficient to produce the observed decrease in attacks on edible, non-mimetic seeds (reviewed by Gilbert and Sutherland, 1969). Novelty might also be involved, since the unpalatable seeds had never been seen before.

In the light of the latter interpretation, punishment, when first experienced, appears able to produce a generalized decrease of attacks toward other, rewarding but not mimetic, components of the situation. A similar phenomenon has been described by Shettleworth (1972) in

Table 19. Comparison over experiments A and B, between attacks on edible seeds in the first session of subphase 2.0 and the first session of subphase 2.2.

Source of variation	Experiment A		Experiment B	
	df	MS	df	MS
Subphase (Su)	1	.1337	1	.22247*
Birds (B)	9	.06508	9	.08515
Su x B	9	.06037	9	.03638

chicks. It would be of some interest to ascertain the extent of such generalization, if indeed the same effects obtain also under natural conditions. With present knowledge, it can only be speculated that such a situation might result in a temporary increase in the mimetic advantage of initial mimetic forms. Such effects would be heightened during the periods of the predators' life when experience is lacking or insufficient, such as the beginning of independent prey selection of fledgling insectivorous birds.

Another point of interest related to these first sessions of exposure to unpalatable seeds can be noticed during the very first session of Subphase 2.0. When initially presented with unpalatable seeds, the birds ate a number without any apparent signs of discomfort or of hesitation. Later, of the few unpalatable seeds that were attacked, practically none were actually ingested. From the initial responses, it appears that initially the effects of distastefulness were not expressed, as evidenced by the very high frequency of attacks on unpalatable seeds measured in the first session (see Figure 5). For animals previously unexposed to any sort of unpalatable food and strongly conditioned to expect reward from the presentation apparatus, such results appear to indicate the possible presence of "expectation" of reward. A further possibility is that the embittering treatment of the unpalatable seeds causes long term after-effects of ingestion (bait shyness).

In either cases, speculations could be made on the basis of these findings with respect to the models and the hypothesized increase in attacks on them due to presence of mimics. If the predators are already familiar with the edible mimics, the time that the models are first encountered may represent a period when a much higher rate of predation, than otherwise expected, would befall the models. Both this and the previously suggested hypothesis could be explored in nature, by examination of times of emergence of mimics and models.

In conclusion, it would seem that the first encounters with unpalatable prey might yield predictable changes in frequency of attacks (on mimics, models and non-mimics respectively) that might not be expected on the basis of existing "mimicry" theories. Even though such effects might only be transient, their importance on an evolutionary scale should not be overlooked.

3.4. DISCRIMINATION LEARNING OVER TIME

Birds are well known for their associative learning abilities, color discrimination, and learned reactions to mimic-models systems. However, different tasks may vary in the length of time required to be learned, and I have no knowledge of detailed studies in this field with my subject species and in comparable experimental conditions.

Furthermore, during the process of learning a decremental effect on the intake of reward could be expected, since the punishment associated with the "wrong" choice, if a choice is made, continues to be experienced until the relevant cues are learned (reviewed by Medin, et al., 1976). For these reasons, I examined Phase 2 to determine the effects of learning processes and the time factors involved.

The experimentally controlled discrimination "cues" were provided by the colors of the associated background for each seed type. In both experiments no differences had been detected for attacks on seeds associated with either colors during the preceding Phase 1 (see Tables 9 and 10). Therefore, detection of significance between attacks on the two color/seeds complexes could be used, I felt, as a criterion for assessing the presence of learned avoidance not based on taste but on cues associated with it.

a) Subphase 2.0.

For this subphase, the first of Phase 2, the results clearly indicate that in both experiments learning had taken place sometime during the first three sessions (Table 20; see Table 10). In the majority of the birds the criterion was reached by the second session, whereas in the first session no significant difference was detected between attacks on the two types of seeds (Tables 21 and 22).

Table 20. Comparison over experiments A and B, between attacks on edible and unpalatable seeds during the first three sessions of subphase 2.0.

Source of variation	Experiment A		Experiment B	
	df	MS	df	MS
Seed types (T)	1	.9302***	1	.13488*
Sessions (S)	2	.1164	2	.18448**
T x S	2	.13286**	2	.05179**
Birds (B)	9	.12025***	9	.07568***
T x B	9	.04012	9	.01784
S x B	18	.05257*	18	.0262*
T x S x B	18	.01733	18	.00842

Table 21. Means and standard error of the proportion of edible and unpalatable seeds attacked in each of the sessions of subphase 2.0 of experiment A. The dotted lines separate pairs of means that have been found significantly different at the 0.05 level. A Duncan's New Multiple Range Test has been used for the data analysed in Table 20, experiment A (1st, 2nd and 3rd session). For the remaining sessions, t-tests have been used to compare contiguous pairs of means.

Subphase	Session Number	N	Mean ± SE	
			Edible Seeds (with green substrate)	Unpalatable Seeds (with orange substrate)
2.0	1st	10	.472±.068	.401±.064
	2nd	10	.446±.095	.161±.029
	3rd	10	.630±.100	.239±.040
	4th	7	.744±.054	.170±.070
	5th	7	.746±.048	.149±.033

Table 22. Experiment B. Means and standard errors of the proportions of edible and unpalatable seeds attacked in each of the sessions of subphase 2.0. The dotted lines separate pairs of means that have been found significantly different at the 0.05 level. A Duncan's New Multiple Range Test has been used for the data analysed in Table 20, experiment B (1st, 2nd and 3rd sessions). For the remaining sessions, t-tests have been used to compare contiguous pairs of means.

Subphase	Session Number	N	Mean ± SE	
			Edible Seeds (with orange substrate)	Unpalatable Seeds (with green substrate)
2.0	1st	10	.363±.052	.378±.060
	2nd	10	.264±.061	.149±.021
	3rd	10	.295±.072	.110±.023
	4th	9	.339±.079	.070±.015
	5th	4	.395±.063	.080±.018

Figure 5 shows, for the last three sessions of this subphase, in each experiment, a trend of increase over time of the edible seeds attacked. The previously detected decremental effects of introduction of unpalatability appears thus to be overridden. Several causal factors might be involved, alone or in combination, among which perfecting of the discrimination learning and perhaps waning of the former responses to punishment. The trend appears less accentuated for Experiment B, where increments over time are not significant (Table 22). For Experiment A, a significant increment is found between second and third sessions and, by the end of Subphase 2.0, "stability" levels appear to be approached (Table 21, $p<.05$).

It is impossible to determine exactly the relative contributions of the many possible causal factors to this differential effect between experiments. The difficulty of discrimination was the same since colors remained unchanged; only the seed-type/color combinations were inverted. In this respect differential rates of learning could be ruled out. The association color/seed-type has already been indicated as a possible contributing factor, even though I suspect it to be a minor one. The major difference at this stage between the experiments appears to be the length of their preceding phases 1. Moreover, in that phase, the birds of Experiment A had had a higher number of exposures to novelty and had experienced more changes of pairs of color

background.

b) Subphases 2.1 and 2.2.

Both experiments were examined, over the testing periods of each seed/color complex, for the existence of learning times covering more than one session, and/or of novelty effects (Tables 23 and 24; see Table 11). The results of the previous analyses failed to demonstrate any such effects. Thus, it appears that either the colors are learned in a very short time (which, in light of the results of Subphase 2.0 appears unlikely), or that they are not a major discrimination factor. However, the changes in color substrate have been shown to affect the frequency of attack. Furthermore, by the end of Phase 2, in Subphase 2.2 the birds were able to discriminate between seeds on sight on the basis of treatment alone (direct seed discrimination; see next chapter). From these results, the treatment of the seeds appears to be the major differential cue for discrimination, and to be learned at an early stage.

3.5. DISCRIMINATION ABILITIES: SUBPHASES 2.1 AND 2.2

In the original planning of the present study, and according to traditional methods of mimicry experiments, I assumed that the edible and the unpalatable seeds were in

Table 23. Comparison between attacks on edible and unpalatable seeds in the four succesive sessions of the color/seed complex Bb + in experiment B (subphase 2.1).

Source of variation	df	MS
Sessions (S)	3	.00101
Seed types (T)	1	4.47365***
S x T	3	.00783
Birds (B)	9	.11243***
S x B	27	.02254*
T x B	9	.1172 ***
S x T x B	27	.01167

Table 24. Comparison between attacks on edible and unpalatable seeds in the two succesive sessions of the color/seed complex W + (color substrate = White) for experiment B (subphase 2.2). Since data are not available for the birds # 17 and # 18 in the second session, these two birds have been completely deleted from this analysis.

Source of variation	df	MS
Sessions (S)	1	.01233
Seed Types (T)	1	1.3738 **
S x T	1	.01184
Birds (B)	7	.15548***
S x B	7	.01759
T x B	7	.06731***
S x T x B	7	.00549

all aspects indistinguishable prior to tasting. Consequently, the only cues for discrimination of mimics and models would have been provided by the differential colors of the associated substrates.

In the course of Subphase 2.1 of Experiment A, I noticed, however, that some of the birds appeared to learn the most difficult discrimination (color pair Violet1/Violet2) in a surprisingly short time. In examining this phenomenon, I suspected that the two types of seeds might have become distinctive following their differential treatments. For this reason a session, not previously included with the design, was run with edible and unpalatable seeds on the same color substrate (Subphase 2.2). The results, successively confirmed in Experiment B, indicated that the two seed treatments could be discriminated, prior to tasting, even in the absence of color cues from the substrate (Table 25; see Table 24).

Shortly after this finding, a study by Terhune (1976) showed similar discrimination abilities in free-living urban birds when presented with quinine treated and untreated pastry baits. This author suggests a "visual, rather than an olfactory basis" for the discrimination and further that "The birds in my investigation made a very fine discrimination: I could not see the quinine on the baits". After comparing carefully the two types of seeds side by side I, on the contrary, could detect slight differences in

Table 25. Comparison, in experiment A, between attacks on edible and unpalatable seeds in the absence of differential color substrates (subphase 2.2, one session).

Source of variation	df	MS
Seed type (T)	1	.56289***
Birds (B)	9	.08842*
T x B	9	.02209

texture and light reflection. The unpalatable seeds also appeared somewhat more orange-tinged than the others (see Table 1). However, the birds were faced with successive rather than simultaneous presentation, a seemingly more difficult discrimination problem (see Medin, et al., 1976, for a review).

Since a bird's sense of smell is usually rather limited (reviewed by Wenzel, 1971) and I could not differentiate between seeds by odor, I would consider scent discrimination as unlikely. Occasionally the birds were observed to remain in the back part of their cages when trays with unpalatable seeds appeared in the opening of the screen, and to move rapidly toward the trays as soon as an edible seed appeared. Considering the short distance and time between successive trays, this type of behavior seems more compatible with a response to visual cues, clearly separated in space, than to scent cues.

In conclusion, direct discrimination of seed types before tasting was evident by the end of each experiment during Subphase 2.2. Such a discrimination may have been present in the preceding subphases (2.0 and 2.1), possibly being the only factor affecting the frequency of attacks, regardless of the two different colors then associated with the seed types.

In the absence of variability due to "contrast" effects of coloration, to learning over time and/or to other

time dependent incremental/decremental influences, the previous hypothesis, that the colors had no significant effect on the discrimination, would lead to a prediction of a continuously stable relationship, throughout the period, between attacks on the two types of seeds regardless of the changes in the colors of the substrates. Accordingly, all the sessions included in subphases 2.1 and 2.2 have been analyzed together, for each experiment, as if no changes in color substrates had taken place during the period considered.

For Experiment A, the frequency of attacks on the unpalatable seeds appears to differ significantly from the previous session's value only for Session 6. The latter was the first, and only, session utilizing the color White. A significant difference was also found, for the edible seeds, between session 2 and 3, at the "boundary" between the color pairs Blue 2/Brown 2 and Violet 1/Violet 2. For Experiment B, if the means are ordered in a time sequence, the unpalatable seeds appear to be differentially attacked during the 5th session compared to the 4th. Again, these sessions are at a "boundary" between two different color pairs (Tables 26, 27 and 28; Figure 6).

In conclusion, not only differences over time (contrary to the stated null hypothesis) were found in the periods considered, but they were also found coincident with changes of color substrates. During Phase 1, findings

Table 26. Comparison, over experiments A and B, between attacks on edible and unpalatable seeds in all the sessions of subphase 2.1 and 2.2 which have data for all ten birds (see tables 4 and 5, also see text).

Source of variation	Experiment A[a]		Experiment B	
	df	MS	df	MS
Seed Type (T)	1	7.05993***	1	4.99831***
Sessions (Sp)[b]	5	.05132	4	.02704
T x Sp	5	.0533 *	4	.02253
Birds (B)	9	.10156***	9	.13941***
T x B	9	.1054 ***	9	.13062***
Sp x B	45	.04746**	36	.03336**
T x Sp x B	45	.01821	36	.01471

[a] - for the reasons given in the text, the two birds' subgroups of experiment A have been grouped together for each session, regardless of whichever color was associated with which seed type.

[b] - Contrary to most other tables, when Sessions (S) has been used to indicate consecutive sessions in respect to color pairs, here the sessions (Sp) are considered in respect to the whole phase 1.

Table 27. Means and standard errors of the proportion of edible and unpalatable seeds attacked during each of the sessions of subphase 2.1 and 2.2 for experiment A. The dotted lines separate pairs of means that have been found significantly different at the 0.05 level by a Duncan's New Multiple Range Test performed on the data of the analysis of table 26, experiment A.

Subphase	Color/Seed Complex [a]	Session Number	N	Mean ± SE	
				Edible Seeds	Unpalatable Seeds
2.1	BB +[b]	1st	10	.773±.045	.232±.055
		2nd	10	.810±.059	.165±.041
	VV +[b]	1st	10	.635±.075	.156±.040
		2nd	10	.663±.096	.196±.069
		3rd	10	.599±.101	.157±.028
2.2	W +	1st	10	.636±.089	.300±.056

[a] - see text for the terminology used.

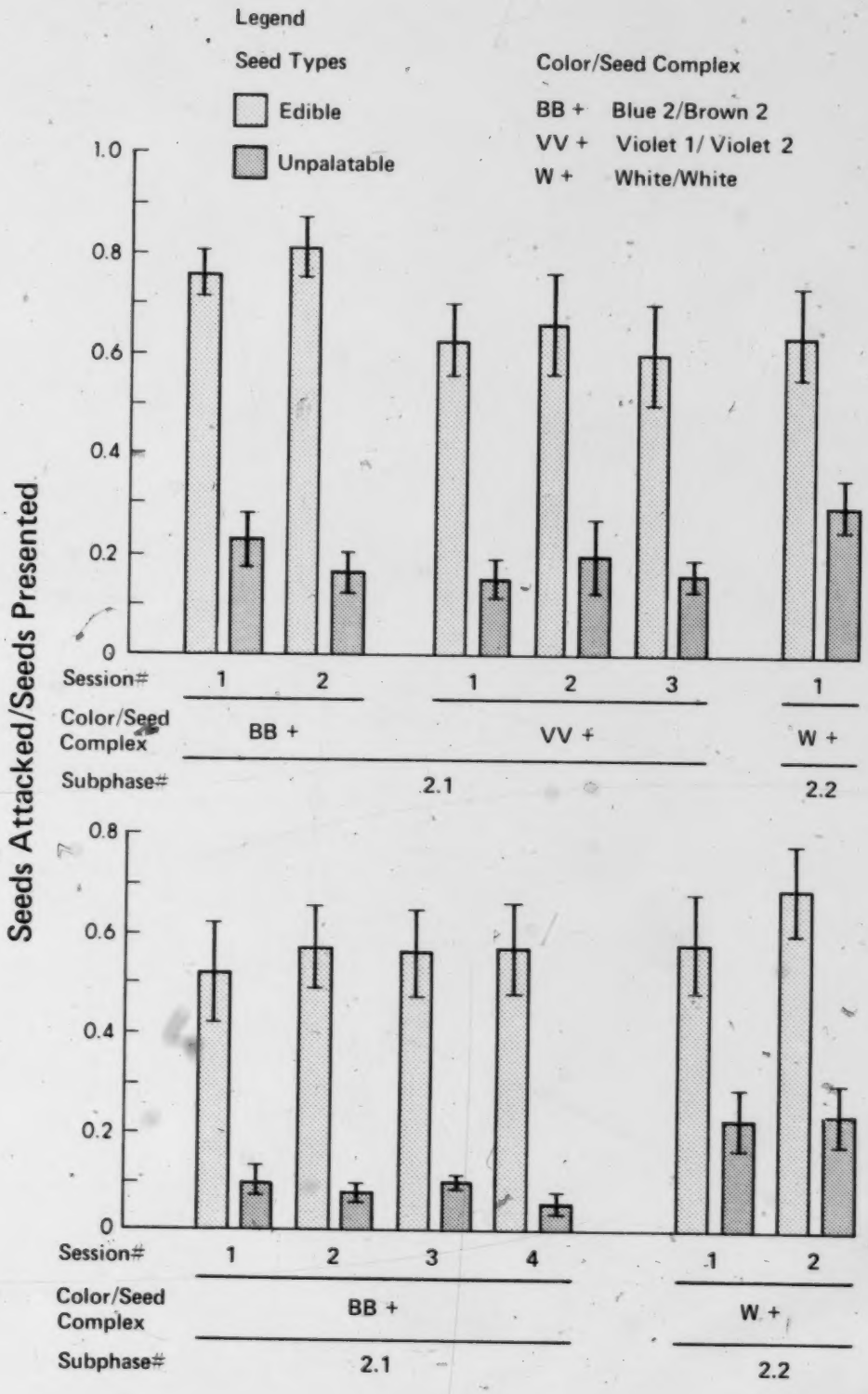
[b] - for the reasons given in the text, the two birds' subgroups of experiment A have been grouped together for each session, regardless of whichever color was associated with which seed type.

Table 28. Means and standard error of the proportion of edible and unpalatable seeds attacked during each of the sessions of subphase 2.1 and 2.2 for experiment B. The dotted lines separate means that have been found significantly different at the 0.05 level. A Duncan's New Multiple Range Test has been used for the data analysed in Table 26, experiment B (cfr. Edwards, 1972, pp. 130-131). For the remaining session (2nd, W +) t-tests have been used to compare contiguous pairs of means.

Subphase	Color/Seed Complex [a]	Session Number	N	Mean ± SE	
				Edible Seeds	Unpalatable Seeds
2.1	BB +	1st	10	.524±.097	.105±.025
		2nd	10	.570±.085	.079±.019
		3rd	10	.564±.085	.093±.015
		4th	10	.570±.088	.060±.019
2.2	W +	1st	10	.574±.097	.230±.059
		2nd	8	.693±.091	.240±.057

[a] - see text for the terminology used.

Figure 6. Means and standard errors for the subphases 2.1 and 2.2. The upper graph refers to Experiment A; the lower to Experiment B. The successive sessions are shown in chronological order for each color pair and subphase.


Legend
Seed Types
Edible
Unpalatable
Color/Seed Complex
BB + Blue 2/Brown 2
VV + Violet 1/ Violet 2
W + White/White
Seeds Attacked/Seeds Presented
1.0
0.8
0.6
0.4
0.2
0
Session#
1
2
1
2
3
1
Color/Seed Complex
BB +
VV +
W +
Subphase#
2.1
2.2
0.8
0.6
0.4
0.2
0
Session#
1
2
3
4
1
2
Color/Seed Complex
BB +
W +
Subphase#
2.1
2.2

apparently similar were attributed to the effects of novelty. However, there differences over time were within the testing periods of each color pair (see Table 13), whereas here no such differences had been detected.

Colors have previously been demonstrated to be among the fastest-learned stimuli for many birds (see Hinde, 1970, for a review). It would, therefore, have been expected that in a situation where a learned avoidance is at a premium, such an obvious cue was utilized by the birds. It can also be considered that most mimetic and model butterflies share a great number of similar characteristics, but also some less similar or completely different ones. For instance, the Monarch and the Viceroy butterflies, notwithstanding their great similarities, differ in some respects. Moreover, the implication of "initial" mimicry hypotheses is that, even though many differences are present and quite conspicuous, very slight, "initial" similarities can be somewhat protective. In this light, even if the seed part of a complex were very distinctive - which might be doubted - the background coloration might provide at least "initial" mimetic characteristics.

3.6. EXPERIMENT C

Experiment C represents an attempt to overcome the problem of direct discrimination of the two types of seeds.

The approach taken was to eliminate completely the treatment of the seeds as a possible cue, by successively presenting the quail with colored keys, keeping the seeds out of view. One seed was dropped into an adjacent tray only after the corresponding key was pecked (Key-tray). The type of seed received by the birds depended upon the key color. It was hoped that the birds would eat or at least taste all of the seeds obtained after pecking at the keys.

A new apparatus was designed for this purpose by modifying the previously-utilized seed presentation apparatus with the addition of keys and of a mechanism for seed distribution (Figure 7). Precautions were taken to avoid giving unintended cues for discrimination. The two glass tubes containing the two seed types, prior to distribution were, for instance, covered from the sight of the bird undergoing the trial, etc.

In this experiment a series of sessions were run, generally following the phases of the preceding experiments (Table 29). A trial consisted of successive presentations to every bird of a total of 104 key-trays over about 15 minutes per daily session. When two colors were tested in the same trial, each color was randomly assigned to half of the keys.

The pre-training period of Experiment C (Subphase 1.0) was much longer than that needed for the previous series of experiments, possibly due to the greater complexity of the

Figure 7. Diagram of the apparatus for presentation of prey in experiment C. The legend and a brief description of the numbered items are presented below.

LEGEND	DESCRIPTION
A. Apparatus	for the presentation of prey
1. Table	
2. Wooden Frame	supports the seed distributor apparatus (B).
3. Opaque screen	
4. Glass tube(s)	contain the seeds (edible on the left, unpalatable on the right) prior to distribution
B. Seed distributor	Only the left part is completely drawn: the right part is symmetrical (see also under A).
5. Bar holder	it constrains the movements of the bar (6) on a straight line, and contains the seeds that drop, one by one, from the glass tube (4)
6. Bar	(Drawn for clarity out of the bar holder (5)) It moves back and forth, controlled by 7 and 8
7. Spring	it calls the bar (6) back after a forward movement
8. String	connects the bar (6) with the pedal (9) by a system of (19) pulleys
9. Pedal(s)	by pressing one of them, the corresponding bar (6) moves forward and it pushes one seed down the plastic funnel (10)
10. Plastic funnel	
11. Glass funnel	it collects the seed dropped from B and it conveys it to 12
12. Glass tube	it conveys the seed to the tray (16, described under C)
13. Support frame	it supports 12 (glass tube)
14. Opening	for key-tray presentation
15. Rotating wheel	rotation of this wheel presents one key-tray at a time to the subject through the opening (14)
C. Key-tray	Key-tray. There are a total of 26 Key-trays on the rotating wheel (15)
16. Tray	the seed is dropped in it
17. Key	it can partially rotate around two hinges that connect it to the tray (16). By lifting it, a piece of colored paper can be placed below, between it and a foam pad (18)
18. Foam pad	it supports the colored paper
19. Pulley(s)	

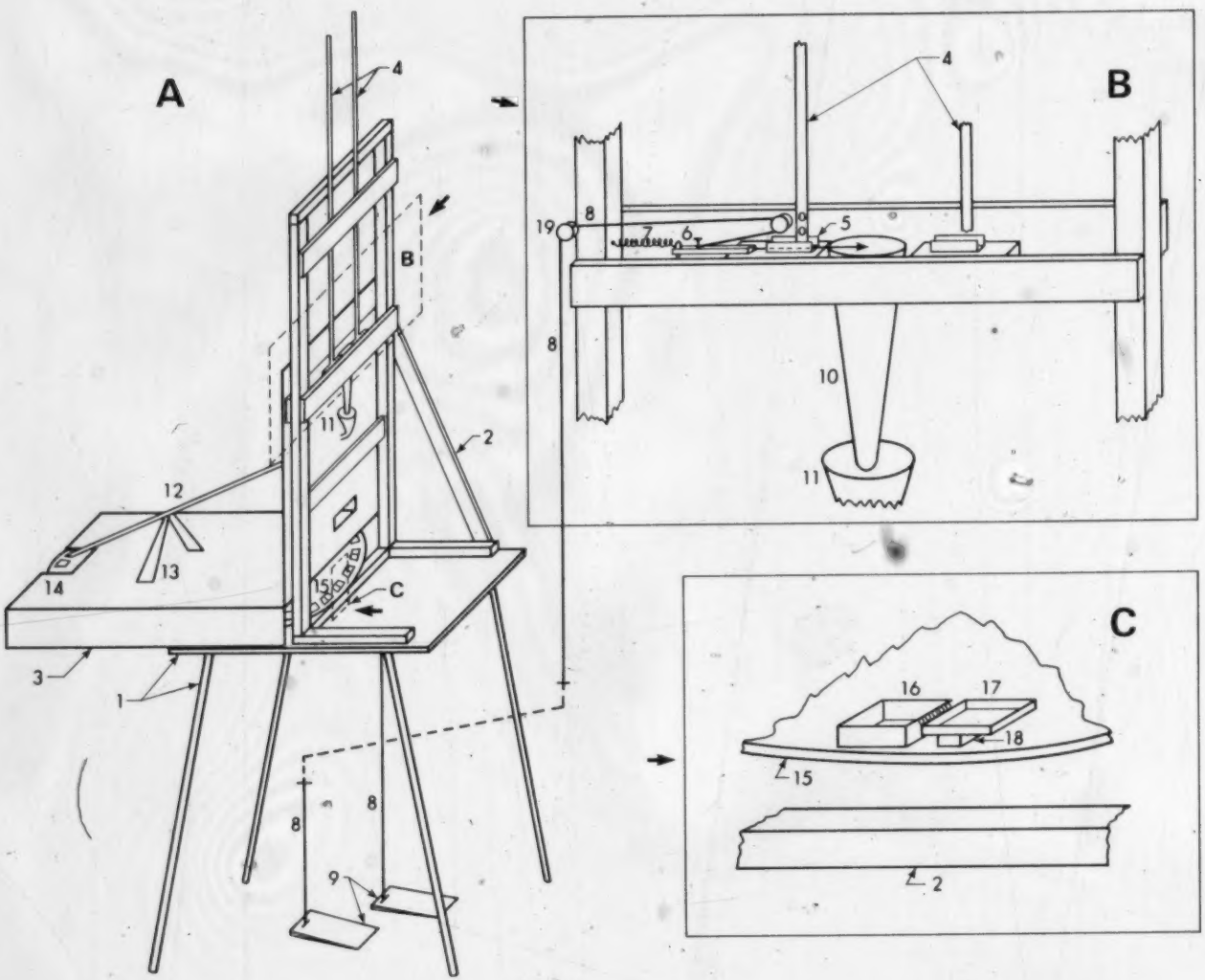

A
4
B
11
2
12
13
14
15
C
3
1
8
8
9
B
4
19
8
7
6
5
8
10
11
C
16
17
18
15
2

Table 29. Experimental plan for experiment C (see text). In every session 4 birds were tested, the same throughout (birds # 3,5,6,10).

Phase #	Subphase #	Color pair #	Key Colors	Number of sessions/Color pair
1. (Edible seeds only)	1.0 Pre-training (only one key color)	1st	White	15
	1.1 (pairs of key colors)	1st	Red/Blue 1	2
		2nd	Orange/Green	1
2. (Edible and Unpalatable Seeds)	2.0 Conditioning (pairs of key colors)	1st	Orange/Green*	3
	2.1 (pairs of key colors)	1st	Red*/Blue 1	5
	2.2 (only one key color)	1st	White*/White	2

* - color associated with the unpalatable seeds.

task to be learned. Unfortunately, one of the ten quail died during the course of the experiment, two fell ill and so were not used, and three, when first presented with unpalatable seeds, failed to peck at the keys. Only four quail, then, were utilized throughout the experiment. For these reasons the data were not completely analyzed, as done for the experiments A and B. I, however, feel that some interesting inferences could still be derived from the results obtained from these four birds.

As observed in the previous experiments, in Phase 1, where only edible seeds were distributed, no preferences for any colors of different pairs (Red/Blue 1 and Green/Orange) were shown (Table 30). In subphases 2.0 and 2.1, when one of two colors was associated with unpalatable seeds, the quail appeared to learn the discrimination, but occasionally they pecked at a key and then failed to attack the unpalatable seed received. On the other hand, practically all the edible seeds received were attacked (Table 31).

These results appear to indicate presence of direct discrimination of the seeds. However, it was still possible that the quail had been so strongly conditioned to peck at the keys, that they pecked even when they "knew" that the associated seed would have been unpalatable. If this were the case, then avoidance of the seed could have been delayed but the decision still based on the color and not on direct perception of the seeds themselves.

Table 30. Seeds attacked during subphase 1.1 of experiment C. Comparisons have been made, for each bird, between seeds attacked and not attacked for the two colors tested in each session (chi square with Yates' correction). No difference has been found to be significant.

Subphase #	Color pair #	Session #	Key Color	Bird 3	5	6	10
1.1 (only edible seeds; pairs of colored keys)	Red/Blue 1 (1st)	1st	Red	39	30	35	47
			Blue 1	38	28	36	41
		2nd	Red	37	31	34	27
			Blue 1	37	33	36	29
	Orange/Green (2nd)	1st	Orange	52	47	32	46
			Green	51	48	33	50

Table 31. Seeds attacked during subphase 2.0 and 2.1 of experiment C. In brackets are the numbers of seeds received but not attacked. Comparisons have been made, for each bird, between seeds attacked and not attacked for the two colors tested in each session (chi square with Yates' correction).

Subphase #	Color pair #	Session #	Key Color	Bird # 3	5	6	10
2.0	Orange/Green (1st)	1st	Green	23	13(1)	14	11
			Orange	27	16	22	14
		2nd	Green	9(4)***	9(2)	3(1)**	15(1)*
			Orange	27	17	14	25
		3rd	Green	17(4)***	7(11)***	9(3)***	5(7)***
			Orange	43	49	38	52
2.1	Red/Blue 1 (1st)	1st	Red	11(11)	11(8)**	12(6)*	8(11)
			Blue 1	19	24	24	15
		2nd	Red	15(10)**	21(12)***	15(2)***	18(23)***
			Blue 1	30	38	36	35
		3rd	Red	6(13)**	14(10)	11(4)*	1(3)
			Blue 1	19	23	23	6(1)
		4th	Red	13(10)***	8*	3***	8(17)***
			Blue 1	29	19	22	36
		5th	Red	13(7)***	10(2)***	10(3)***	
			Blue 1	33	37	30	

*** - $P < 0.005$

** - $0.005 < P < 0.01$

* - $0.01 < P < 0.05$

To clarify this last point, two further trials were run with all the keys of the same color, half of which were associated with unpalatable seeds (Subphase 2.2). Quail #6 apparently failed to discriminate between the seeds; the other three birds, after having pecked at the keys and received the prey, refused to attack unpalatable seeds significantly more often than the palatable ones (Table 32). It seems evident that some quail are able to solve, at least in part, this last discrimination problem by utilizing cues from the seeds and ignoring, or bypassing, the cues provided by the colored keys. These results demonstrate that even this technique is not foolproof.

Table 32. Unpalatable and edible seeds attacked (A) and received but not attacked (R), during subphase 2.2 of experiment C. Comparisons have been made, for each bird, between A and R in each session (chi square with Yates' correction). The key colors were the same for both seed types.

Subphase #	Session #	Type of Seed	Bird # 3 A	3 R	5 A	5 R	6 A	6 R	10 A	10 R
2.2	1st	Edible	19	15_{***}	29	14_{***}	17	3	11	18_{***}
		Unpalatable	37	0	37	0	21	0	35	0
	2nd	Edible	13	23_{***}	15	8_{***}	14	2	17	21_{***}
		Unpalatable	36	0	24	0	29	0	41	0

*** - $p < .005$

4. ESSAY OF SYNTHESIS: MIMETIC RESEMBLANCE

The original intent of this study was to examine the properties of an artificial model involving presentations of progressively better mimics to caged birds. I was aware, however, that a number of other factors, beside mimetic resemblance, could affect pecking rates and that their uncontrolled presence could mask the effects of mimetic resemblance itself. In attempting to control for these factors, I successively added to the design several components, so as to reach the final stage with unconfounded mimicry effects.

First, I introduced the birds to the experimental basic parameters, such as seeds, hunger, apparatus for presentation of seeds, etc. (Subphase 1.0). I then introduced coloration into the model, by presenting the birds with pairs of color substrates (Subphase 1.1). No differences could be evidenced between effects of different colors, per se, within each color pair, not even for the most "cryptic" background. However, the changes in color substrates ("novelty" effects) appeared to originate significant decrements in attacks on the edible seeds presented. By the end of Subphase 1.1, such effects appear to have been reduced to non-significance ("stability" levels) in Experiment A. In Experiment B, this process of recovery from novelty effects appears incomplete: by the end

of its Subphase 1.1, carry-over effects could still be present.

In the successive Subphase 2.0, I introduced unpalatability to the birds. They had not been trained to expect punishment from the apparatus and, consequently, reacted by dropping attacks on seeds to a very low level in both experiments. However, in Experiment A the drop in edible seeds attacked appeared reversible, and by the end of the session, the experiment appeared nearly free of carry-over effects related to the introduction of unpalatability. In Experiment B only signs of recovery were shown, and by the end of Subphase 2.0 still very low levels of attacks on edible seeds could be found. For the unpalatable seeds, they appeared to be attacked, in both experiments, more during the first session of exposure than in the successive ones.

In Subphase 2.2 I noticed that, somewhere along the progression of Phase 2, the two seed types had been learned as distinctive without tasting and in absence of color substrate differences. Consequently, Subphase 2.1 and Subphase 2.2 (the ones I was interested in for the mimetic problems I wanted to investigate), were examined for indication of overriding, *via* the discrimination of the seeds *per se*, the possible effects of mimetic similarity. Such possibility did not appear to occur in either experiment, since changes with time were found between pairs

of color substrates, but not within them. Therefore, such changes appear to be derived from the presence of effects of mimicry that were introduced in both subphases 2.1 and 2.2.

For Experiment A, contrary to Experiment B, I could at this stage be fairly confident that the results of these subphases were not influenced by confounding carry-over effects of the other parameters examined. Therefore, I will examine the two experiments separately, for demonstration of mimetic effects of increase in similarity between mimics and models, in Experiment A, and for the combined effects of previous experience not sufficiently prolonged, in Experiment B.

Tables 33 and 34 show the statistical tests that the following discussion is based upon. In these tables and following figure, for each experiment I have lumped together all sessions of each seed type for each color/seed complex. The resulting values, supposedly reflecting the contribution of "mimetic" effects, have been indicated with symbols that represent both the corresponding substrates' coloration (with the initials of the colors) and unpalatability (with a plus). Thus, BB+ stands for the least resemblant mimetic pair (with the Blue 2/Brown 2 substrates); VV+ for a more resemblant pair (with the Violet 1/Violet 2 substrates), and W+ for the most resemblant mimetic pair tested (with White as the substrate for both seed types).

Table 33. Comparison between seeds attacked in the various color/seed complexes of subphase 2.1 and 2.2, over experiments A and B. Edible and unpalatable seeds are considered separately. For each complex and seed type, all the measurements obtained during the different sessions, if any, are grouped and analysed together (N). The upper part of the table contains comparisons made within experiment A; the lower, experiment B. The symbols used are explained in the text; means are presented as the proportions of seeds attacked.

Experiment	Color/Seed Complex	N	Edible seeds			Unpalatable seeds		
			Means	t value[a]	P	Means	t value[a]	P
A	BB +	20	.792	2.537	<.05	.199	0.663	NS
	VV +	30	.632			.170		
	BB +	20	.792	1.622	.04<p<.05	.199	1.554	.04<p<.05
	W +	10	.636			.300		
	VV +	30	.632	0.030	NS	.170	2.107	<.05
	W +	10	.636			.300		
B	BB +	40	.557	0.873	NS	.084	3.611	<.01
	W +	18	.627			.234		

[a] - one-tailed test.

Table 34. Comparison between experiments A and B of seeds attacked when in the same color/seed complexes. Edible and unpalatable seeds are considered separately. For each complex and seed type within each experiment, all the measurements obtained during different sessions (if any) are grouped and analysed together (N) (see text). The symbols used are explained in the text. Means are presented as the proportion of seeds attacked.

Color/Seed Complex	Experiment	N	Edible seeds			Unpalatable seeds		
			Means	t value	P	Means	t value	P
BB +	A	20	.792	4.117	<.01	.199	3.212	<.01
	B	40	.557			.084		
W +	A	10	.636	.080	NS	.300	0.957	NS
	B	18	.627			.234		

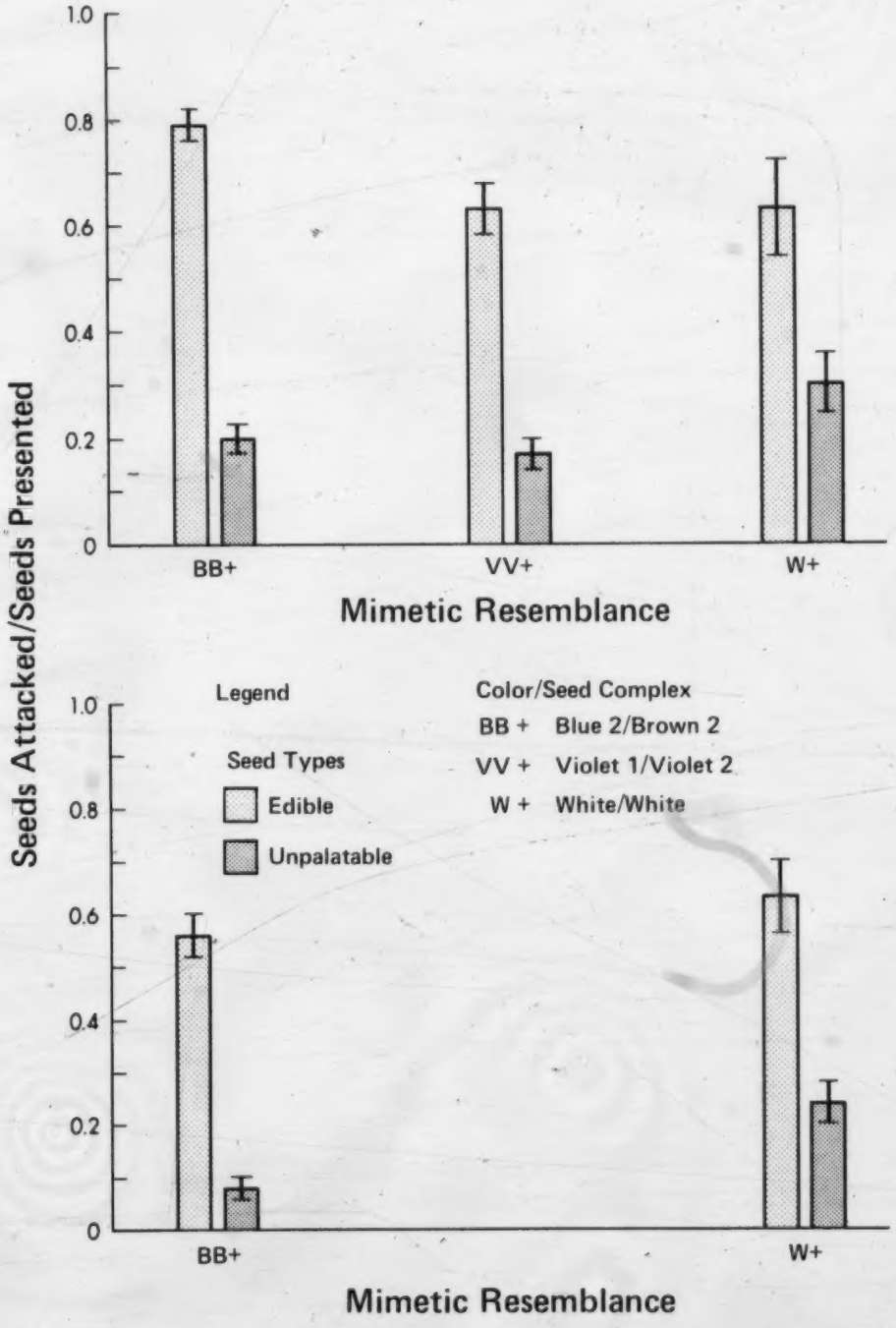
a) Experiment A

In Figure 8 the results of Experiment A are plotted against a mimetic resemblance gradient of the type described by Figure 1.

The presence of an originally unsuspected component of discrimination (direct discrimination of the seeds per se), appears to decrease the expected amount of "mimetic resemblance" between the color pairs tested. A supposedly "perfect" mimetic pair, involving the same color substrates for the two types of seeds, appears in combination with such seeds not to be "perfect" mimicry any more. In the absence of a more precise definition of the exact degrees of mimetic resemblance, I reserved judgement on the positioning, in Figure 8, of the color pairs tested. The only characteristics maintained are the relative positions. These same considerations will apply when discussing Experiment B.

As seen in Figure 8, mimetic factors appear to significantly protect a better mimic (VV+) in respect to the worst mimic tested (BB+). This lower frequency of attack is shown also for the best mimics (W+), but only with respect to the worst ones. These latter results, whether representing a true lack of differences or one too slight to be detected, appear to provide some evidence in support of Duncan and Sheppard's hypothesis (1965), suggesting non-linearity of the effects of changes in mimetic

Figure 8. Means and standard errors of each seed/color complex in subphases 2.1 and 2.2, represented against a gradient of "mimetic resemblance" (see text). The upper graph refers to Experiment A; the lower to Experiment B.


1.0
0.8
0.6
0.4
0.2
0
Seeds Attacked/Seeds Presented
BB+
VV+
W+
Mimetic Resemblance
Legend
Seed Types
Edible
Unpalatable
Color/Seed Complex
BB + Blue 2/Brown 2
VV + Violet 1/Violet 2
W + White/White
1.0
0.8
0.6
0.4
0.2
0
BB+
W+
Mimetic Resemblance

resemblance (see chapter 1.d). Indeed, a similar effect is shown, in reverse, for the unpalatable seeds: with increases in similarity, the former seeds appear not to be differentially attacked until the best mimetic stage (W+) is reached. The fact, however, that such a significant increment is shown, is in itself an interesting result, considering the general lack in the literature of experimental demonstration of this part of mimicry theory.

The points on my graph (Figure 8) are too few, and the uncertainties in their positioning too great, to allow for further speculations about the shapes of possible curves. However, it seems evident that, for the mimics and the models, the major mimetic effects do not first appear at the same point of their respective curves. More precisely, these two points appear to be located each on one side of the intermediate mimetic pair (VV+).

b) Experiment B

In Figure 8 the values relative to this experiment are shown in comparison with those of Experiment A. Here, the previously observed increase in attacks on the model with better mimicry is retained; however, the reverse effect on the mimic is not. The confounding presence of carry-over effects of the previously encountered components of variability appears not to allow for the expected protection

of a better mimic.

These results, different from those observed in Experiment A for the same color pairs, indicate that it is indeed imperative to control for the many other aspects of the experimental situation. Undetected, they may be the causal factors of effects sometimes labelled as mimicry.

The behavioral mechanisms involved in mimetic protection, and the psychological factors affecting them, are as yet poorly understood. From the results of my experiments, I feel that some analogies might be made between the former and the "novelty" effects. Both seem likely to stem from similar forms of "fear" of a potential punishment. The difference would be that, in the "novelty" case, the potential punishment never materializes, which would gradually reduce the effects of fear. In the case of mimicry, renewed encounters with the model, even without tasting it, may act as a strong reinforcement. If this is repeated often enough, the effects of fear might not disappear with time.

5. GENERAL CONCLUSIONS

It is unfortunate that only seldom are comprehensive analyses performed in published mimicry studies, when much more information can be derived from such an analysis.

From the results obtained there are indications that a number of factors, other than "mimetic", might affect the outcome of this type of experimentation. "Novelty" effects, as defined by Coppinger (1969), have been found associated with a number of potentially diverse factors such as color, routine change, experimental design and unpalatability (as a novel experience). In particular, the last factor seems to be responsible for an apparent protection of edible forms when the model was first encountered. Mimicry could not easily be invoked, since the cues for the two types of prey were considerably different. The importance of adequate controls is stressed for color preferences, "emotionality" and "motivational" factors, as well as the need for a more precise and standard terminology.

A second finding of this study is that, under certain circumstances, some birds can use slight differences resulting from quinine treatment as cue for discrimination between unpalatable and edible prey without having to taste it or to cue on the colors of the substrate. The quinine treatment has been consistently used in mimicry experiments, with the underlying assumption that it was not a part in the

discrimination process. The assumption is clearly unwarranted by these results and by Terhune's work (1976) and may require that previous studies be critically revised.

With respect to more general theoretical considerations, one contribution of this study seems to be the corroboration of the hypothesis, as yet scantily supported, of an increase in attacks on the models in the presence of close mimics (as hypothesized by Fisher, 1930).

Also, variations with time of a predator's responses to the mimic-model system have been noticed. I have suggested that under more natural conditions the periods of the predators' life history, when experience is lacking or insufficient, might represent a temporary increase in the mimetic advantage, perhaps more so for the initial mimics. A non-linear relationship between increase of mimetic resemblance and frequency of attacks on both models and mimics has also been suggested, pending further experimental evidence.

Finally, I have suggested that in certain cases it might not be possible or easy to make the distinction between "novelty" and "mimicry" effects. Furthermore, the latter effects can be affected by the levels of motivations, such as hunger drive or fear, and/or by the level of arousal. It could then be possible to take advantage of the extensive psychological research done in these fields. Also generalization gradient studies, and extinction and/or

reinforcement studies seem to be very pertinent to a better understanding of the parameters involved in mimic-model-predator systems.

A more complex design, involving key pecking, was also tested in an attempt to suppress the effects of quinine treatment discrimination. The keys, however, appeared to be pecked at random and decision to attack only followed visual exposure to the seed. Thus, the problem of eliminating this component of discrimination appears to require complex solutions.

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